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ZOOLOGY
Vol. 23
1972

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1. INTRODUCTION

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LONDON: 1972

THE GUNONG BENOM EXPEDITION 1967

1. INTRODUCTION

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BY

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School of Biological Sciences
University of Malaya

Pp. 1–7; 4 *Plates*, 2 *Text-figures*

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ZOOLOGY Vol. 23 No. 1

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THE GUNONG BENOM EXPEDITION 1967

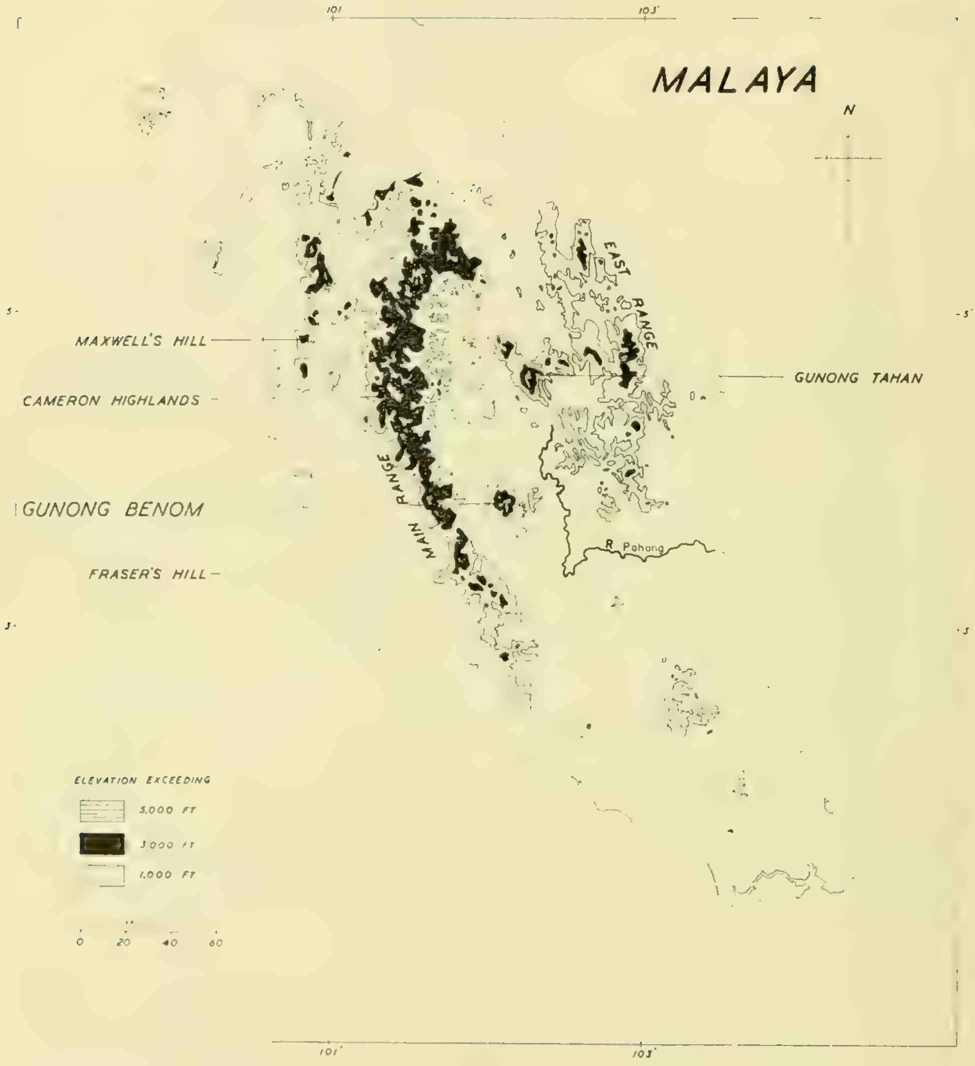
1. INTRODUCTION

By LORD MEDWAY

Apart from relatively narrow coastal plains of Quaternary or Recent alluvium on both flanks of the peninsula, the topography of Malaya (= West Malaysia) is generally hilly or mountainous. About 40 per cent of the total land area rises above the 500 ft contour, and 23 per cent above 1000 ft (Panton, 1965). The principal mountain formations occur as a series of approximately parallel ranges striking north-northwest/south-southeast (Fig. 1). The largest of these, generally called the Main Range, forms a continuous ridge extending from the border of Perak state with Thailand to southern Negri Sembilan. In its northern sector several peaks rise to over 7000 ft, the highest being Gunong Korbu (7160 ft). Further south the elevations attained become progressively lower. The highest mountain in Malaya, Gunong Tahan (7186 ft), is not part of the Main Range, but rises from rugged hill country further to the east in an isolated position on the border of the states of Pahang and Kelantan. Still further eastward an irregular group of lower mountains collectively form the Eastern Range (Fig. 1).

In the centre of the country between the Main Range and the Eastern Range, situated on the right bank of the River Pahang just south of 4°N, lies the compact montane formation named after its highest peak, Gunong Benom (6916 ft) (Plate 1). Here the total extent of connected highland terrain exceeding 3000 ft in elevation amounts to about 75 square miles. These uplands are separated from neighbouring areas of comparable elevation by intervening lowlands. Southwards, the Benom formation is limited by the extensive lowlands of central Pahang. To the west it is divided from the highlands of the Main Range, about 20 miles distant at the nearest point, by the valleys of two tributaries of the River Pahang, one south-flowing and the other north-flowing, between which the watershed lies a little below 500 ft elevation. To the north and east, lower and more extensive valleys of the River Pahang itself and its major tributaries intervene between highland elevations on Gunong Tahan, 47 miles distant, and the Eastern Range, 52 miles distant at the nearest point.

On its south-eastern quarter, a large segment of Gunong Benom extending from the lowlands to the peak is incorporated into the Kerau Game Reserve. Here, and in fact continuously over a much more extensive area of the mountain, the natural vegetation has survived inviolate and the native fauna has been largely protected from hunting and other human disturbance. Benom thus offers the rare opportunity to work in virgin forest along an altitudinal transect from the lowlands to a mountain peak that is among the highest in Malaya.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MALAYA
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CAMERON HIGHLANDS
GUNONG BENOM
FRASER'S HILL
GUNONG TAHAN
EAST RANGE
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FIG. 1. Malaya (= West Malaysia), showing the principal mountain formations.

Accounts of earlier ascents of Benom have been published by Barnes (1903), Evans (1924), Henderson (1927), and Strugnell and Willbourn (1931). On some of these expeditions animals were collected, and the resultant specimens have been listed or described by several authors, *e.g.*, Chasen & Kloss (1928), Gibson-Hill (1949). Despite this, no previous expedition was primarily zoological in purpose. Accordingly, in early 1967, a trip was planned with the principal aim of establishing sites for zoological collection and observation along a transect from the base to the summit of the mountain.

The expedition proper was in the field from 1 February to 15 April 1967. Later return trips to the area were made by several participants resident in Malaysia, as detailed in individual reports (below). Teams from the following organizations participated: British Museum (Natural History), comprising Miss A. G. C. Grandison assisted by Miss F. V. Slade; University of Malaya, Department of Zoology, comprising Lord Medway, H. S. Yong, P. H. Soo, L. C. Ratnam, Miss S. E. Ang, Miss M. C. Leong and D. Labang; University of Malaya, Department of Parasitology, C. P. Ramachandran assisted by K. C. Lim and Poopala Chelvam; University of Malaya, Mosquitoes of Malaysia Project, O. Sulaiman and S. W. James; the Arbovirus Research Unit of the Hooper Foundation, University of California International Center for Medical Research and Training, N. J. Marchette, R. Garcia, and D. W. MacVean, assisted by J. Jeffery, H. Lee, Miss S. K. Teh, A. H. Ahmad, Nagiah Vangitasamy, S. W. Chan, T. K. Tee and R. de Silva; Institute for Medical Research, Kuala Lumpur, B. L. Lim and M. Nadchatram, assisted by P. Ramachandran, K. Krishnaswamy, A. Mottan, B. Ahmad, M. Sharif, W. Mohamed, R. S. Ratnam and I. Yusof; Forest Research Institute, Kepong, Selangor, T. C. Whitmore assisted by Chelliah, I. Rahim and Y. Zahir.

THE ENVIRONMENT

Base Camp was established just within the Kerau Game Reserve, on the bank of a south-flowing tributary of the River Kerau, at 102°11′25″E, 3°51′30″N, at 700 ft above sea level (Grid reference 097 667 on sheet 79, Malaya 1:63,360, series L7010). Access from the Damak-Ulu Cheka road was by an abandoned logging track. This track ran through State Forest Reserve, consisting of tall forest recently disturbed by selective commercial felling, which had been carried out as far as the camp site but had not extended across the stream (Plate 2).

From Base camp the route up the mountain followed the succession of ridges that form the north-east boundary of the Kerau Game Reserve (Fig. 2). Camps and collecting areas were established along this route at the following sites: camp 2 at grid reference 081 667, 1700 ft a.s.l. (Plate 3); camp 2½ at 063 666, 2500 ft; camp 3 at 055 661, 3500 ft; camp 4 at 035 653, 5000 ft; and camp 5 at 015 645, 5900 ft.

The parent rock of Gunong Benom itself is an intrusive hornblende-granite, with exposures of syenite, pyroxene-granite prophyry, and diorite (Scrivenor, 1931). On the north-east approach followed by the expedition, sedimentary rocks of Triassic age, with some admixture of Quaternary volcanic effusives, extend to over 1000 ft (Alexander, 1965). At higher elevations, as far as is known, the geology of the mountain is relatively uniform and the main factors affecting the vegetation are therefore not geological but related to local variations in elevation, aspect and climate. The altitudinal zonation of the forest in which the expedition worked on the north-east slopes of Benom is described and discussed by Whitmore (1972).

The route to camp 2 was a relatively easy slope following an abandoned logging track running between the trunks of standing forest giants on a broad ridge. Except after a lot of rain, it could be negotiated by Landrover, sometimes requiring the aid of chains.

From camp 2, the path immediately climbed steeply to a long undulating ridge at 2400–2500 ft. At the time of the expedition, logging had not extended above 2000 ft on this slope. Camp 2½ was sited at the further end of the ridge, at the foot of a second steep climb to 3500 ft and camp 3.

From camp 3 the track climbed by a series of narrow undulating ridges. Camp 4 was located on such a ridge, with unstable, boulder-strewn slopes dropping away precipitously on each side. Above about 3500 ft, many large granite boulders were exposed on the hillsides. Between these, the ground surface was very irregular and in many places damp tunnels and rock shelters were formed. Camp 5 was sited under the overhang of an exceptionally large boulder, at the north-western end of an extended ridge rising to 6300 ft. Beyond this ridge, the path dropped to below 6000 ft before climbing again to the summit ridge proper. The first peak on the summit ridge rose to 6760 ft. Between this peak and the true summit (6916 ft) the path wound round, up and down a series of subsidiary crests and knolls (Plate 4). On the summit itself a survey beacon had been erected. The surrounding vegetation had been felled and, at time of our visit, the regrowth had recently been cut back.

Climatically, Benom lies within the West Rainfall Region (Dale, 1959), at the northern extreme of the central south dry belt. The mean annual rainfall is inferred to be in the range 80–90 inches, distributed in two maxima (October/November and April) and two minima (July and February) each year. Rainfall records were not kept during the expedition, and nothing is known of local variations in precipitation on the mountain. During most of the month of March 1967, we experienced a spell of fine dry weather, which was probably not untypical. At higher elevations surface water was scarce, but streams flowing largely or completely underground were found up to 5750 ft.

Air temperatures were not recorded on Benom during the expedition, and there is no meteorological station on the mountain. The equatorial position of Malaya coupled with a generally humid climate prevent wide variations in surface temperature. Annual mean temperatures recorded at 58 stations in the lowlands fall within the range 77 83°F, and diurnal variations rarely exceed 22°F (Dale, 1963). At most stations there is a discernible pattern of seasonal variation in monthly mean temperature, but the annual range of this variation is small, not exceeding 3·8°F at lowland stations (4·1°F at Fraser's Hill). With increasing altitude there is a

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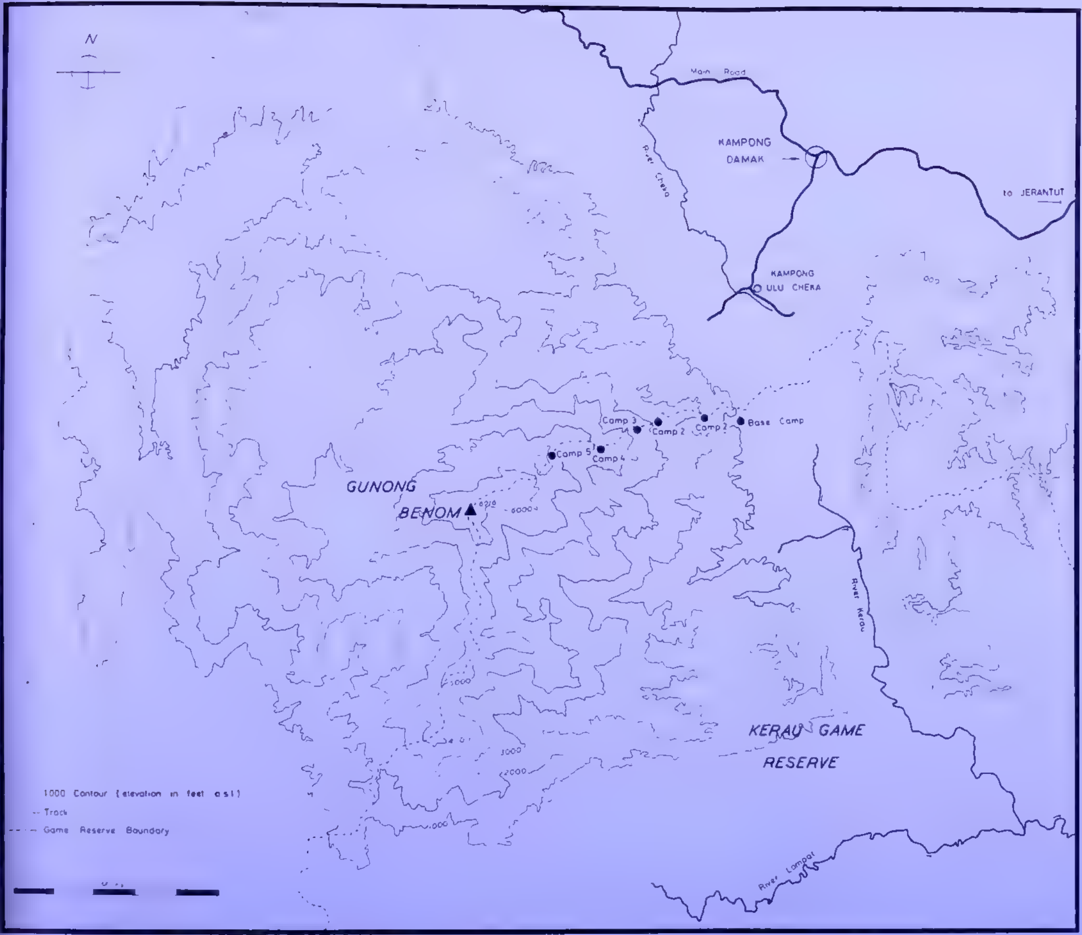
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River Chera
KAMPONG DAMAK
to JERANTUT
KAMPONG ULU CHERA
Camp 3
Camp 2
Camp 2
Base Camp
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Camp 4
GUNONG BENOM
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1000
3000
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1000
River Kerau
KERAU GAME RESERVE
River Lompat
1000 Contour (elevation in feet a.s.l.)
Track
Game Reserve Boundary

FIG. 2. Gunong Benom, showing the expedition camp sites and route of ascent.

regular decrease in temperature, but freezing level in the atmosphere, at 13,500–15,500 ft, is as high again as the highest mountain, so that very low temperatures nowhere occur (Dale, 1963). At most hill stations, the range of diurnal variation is low. Most members of the expedition felt distinctly cold at camp 5, and here and at camp 4 we burned fires at night for warmth.

ACKNOWLEDGEMENTS

Overhead costs of the University of Malaya, Department of Zoology team, including preliminary reconnaissance and the establishment of camps and working sites, were met in chief by a grant from the British Museum (Natural History). Permission to operate within the bounds of the Kerau Game Reserve was kindly given by the State Game Warden, Pahang, who also suggested the site for Base camp, and provided generous assistance in the early stages of setting up this camp.

The participation of the Arbovirus Research Unit, UC-ICMRT, was partially supported by U.S. Public Health Service Grant No. TW 00144 of the Office of International Research, U.S. National Institutes of Health and by the U.S. Army Medical Research and Development Command under Contract No. DA-49193-MD-2931.

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Suffolk, U.K.

Photographs by Lord Medway

PLATE I

The Damak–Ulu Cheka road, with a distant view of Gunong Benom from the north-east.

PLATE 2

Base camp. Note the dense stand of *Mallotus paniculatus* and other secondary vegetation on the edge of the clearing.

PLATE 3

The site of camp 2 at 1700 ft. Very little disturbance of the natural vegetation had occurred

PLATE 4

The summit ridge of Gunong Benom, looking west-southwest from 6760 ft towards the true summit (centre background).

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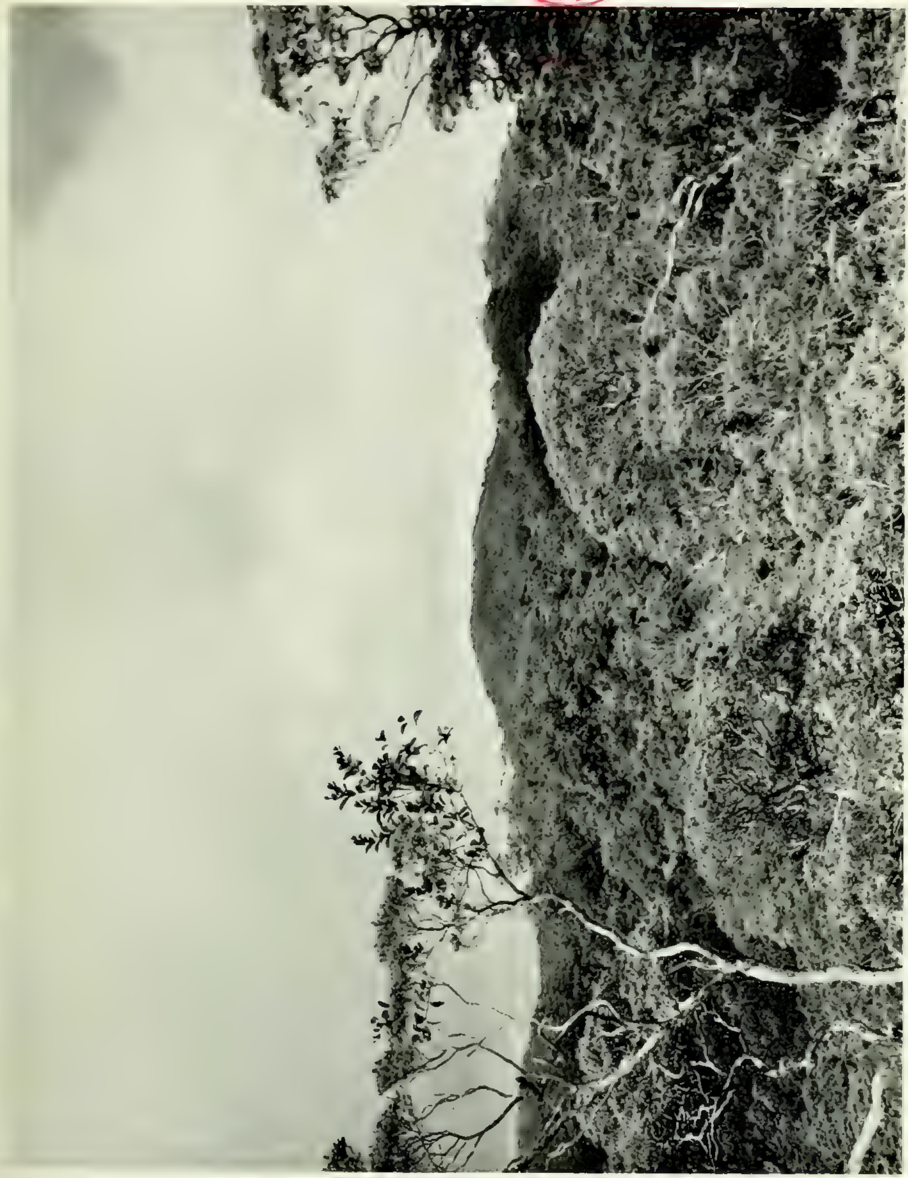

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1. Kay, E. Alison. Marine Molluscs in the Cuming Collection British Museum (Natural History) described by William Harper Pease. Pp. 96; 14 Plates. 1965. (Out of Print.) £3.75.
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THE GUNONG BENOM EXPEDITION
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2. AN OUTLINE DESCRIPTION OF THE FOREST ZONES ON NORTH-EAST GUNONG BENOM

T. C. WHITMORE

3. BRYOPHYTES AND FILMY FERNS FROM GUNONG BENOM

ANNE JOHNSON

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BY

TIMOTHY CHARLES WHITMORE
Forest Research Institute, Kepong, Malaysia

3. BRYOPHYTES AND FILMY FERNS FROM GUNONG BENOM

BY

ANNE JOHNSON
Nanyang University, Singapore

Pp. 9-20; 8 *Plates*

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THE GUNONG BENOM EXPEDITION 1967

2. AN OUTLINE DESCRIPTION OF THE FOREST ZONES ON NORTH-EAST GUNONG BENOM

By T. C. WHITMORE

THE north-east ridge of Gunong Benom provides in a single majestic sweep a fine locus, perhaps the best in Malaya, for the study of the change of forests with elevation. Above about 1000 ft the rock is uniformly granite and the ridge is broad and more or less continuous. Therefore there are no complications introduced by changes in geology or by broken relief.

In 1967 Kepong botanists spent about four weeks plant collecting on Benom, part of the time with the University of Malaya/British Museum (Natural History) Expedition. I myself also made an outline survey of the vegetation types. This I describe here to set the picture for the more particular studies made by the varied groups of zoologists on the Expedition. I hope that publication of this background will stimulate a forest ecologist to visit Benom to make a detailed study of the phenomenon of the altitudinal zonation of tropical forest, for which this mountain is ideally suited.

Tropical rain forest altitudinal zones may be classified in two ways. Firstly we may distinguish Rain Forest Formation Types, defined on structure and physiog-

TABLE 1

ALTITUDINAL FOREST ZONES IN MALAYA (AFTER SYMINGTON, 1943)

Malayan floristic zones	Elevation	World-wide structural and physiognomic zones
Lowland Dipterocarp		
	c. 1000 ft	Lowland Rain forest
Hill Dipterocarp		
	c. 2500 ft	
Upper Dipterocarp		
	c. 4000 ft	Lower Montane Rain forest
Montane Oak		
	c. 5000 ft	
Montane Ericaceous		Upper Montane Rain forest

Bull. Br. Mus. nat. Hist. (Zool.) **23**, 2.

nomy, and recognizable throughout the humid tropics. Secondly we may define zones on flora; these are consequently restricted to a particular country or region. These two classifications run together, as set out in Table 1. Further description of the Formation Types is given in Grubb *et al.* (1963).

The Malayan floristic zones were described and defined by Symington (1943), and have been redescribed and amplified several times by Wyatt-Smith (notably Wyatt-Smith, 1964).

The forest at about 700 ft around Base camp is Lowland Rain forest, and floristically is very rich Lowland Dipterocarp forest. There had been selective logging of the most valuable timber, including many of the dipterocarps, a few months before we visited Benom, so it is no longer easy to give a floristic account of the area. Logging did not extend west of the river Kerau. The area east of the Kerau had relict tall trees isolated or in groups, and the main and lower parts of the forest canopy was variously broken or disturbed by extraction tracks etc.

Before disturbance the original forest had been magnificent, as witnessed by the still standing trees of *Koompassia excelsa* (Leguminosae), with its fluorescent green, smooth trunk and cauliflower-shaped crown, reaching 150 to 200 ft or even taller (Plate 5). Here we felled a relict 150 ft tree which proved to be *Kibatalia arborea*, only otherwise known in Malaya from a few trees at Kepong and one in Ulu Langat. Further details of the flora of this zone can be found through Appendix 1.

In the open places left by timber extraction, for instance around the camp, a dense stand of *Mallotus paniculatus* (Euphorbiaceae) had grown up with some *Sapium* (Euphorbiaceae) and some *Macaranga gigantea* (Euphorbiaceae). In other places dense thickets of gingers and wild banana had sprung up along extraction tracks (Plate 6).

The unfelled forest across the stream was typical of many valley bottoms, some high forest with riverine species, e.g., *Dillenia reticulata*, and some scrub and climber thickets. There was little bamboo. An old *Rafflesia hasseltii* flower was found in one scrub thicket. South of the camp were patches to an acre or so in extent of the scrambling fern *Gleichenia* (*s.l.*) with secondary forest trees growing through; these areas are probably sites of former aborigine cultivation. Although all human settlements were moved a few years ago to Kuala Lompat, outside the Game Reserve, the map given by Ogilvie (1949) shows both Negrito and Jah Chong people on north-east Benom. Similar *Gleichenia* patches and rattan tangles on the steep west slope of the Kerau valley have probably resulted spontaneously from landslips.

Felling had continued, but less intensively, on the hill slope up to camp 2 at 1700 ft. Larger patches of original forest remained, and the track from Base camp ran amongst standing forest giants (Plate 7). Along this track and above camp 2 felling had been restricted to the north side, outside the Game Reserve. Since the Expedition was in the field, extensive felling in 1968 has covered a large area here, up to and abutting on the Game Reserve boundary along the main north-east ridge, and there has been some encroachment.

The undisturbed forest begins almost at once above camp 2. The ridge to camp 2½

(2500 ft) carries very fine Hill and Upper Dipterocarp forest. *Shorea curtisii* (Dipterocarpaceae) is prominent, associated with *Shorea maxwelliana* and a *Swintonia* (Anacardiaceae). Isolated big trees of the conifer *Agathis dammara* were seen. *Eugeissona tristis*, a big undergrowth palm commonly associated with *S. curtisii*, is absent.

Between 2500 ft and 3500 ft a sharp and almost total change in flora occurs. This is associated with a change to Lower Montane Rain forest, within which camp 3 lay. The change in forest type can be clearly seen on aerial photographs.

At camp 3 the forest was described as follows* (and following the scheme in Table 10 in Grubb *et al.*, 1963):

3500 ft	Broad ridgetop
Canopy:	70–80 ft, the biggest trees 8–9 ft girth, with tall straight boles, amongst them *Adinandra* (Theaceae), *Santiria rubiginosa* (Burseraceae) and *Tristania* (Myrtaceae) prominent (Plate 8).
Climbers:	Photophytes: none seen. Skiophytes: *Freycinetia javanica* (Pandanaceae) and another *Freycinetia sp.* frequent.
Epiphytes:	Vascular: infrequent; non-vascular: 10% thin cover on tree trunks; 20%, or rarely up to 90%, cover up to 6 ft on butts.
Soil:	Continuous leaf litter, over a spongy 6 in. peat layer itself overlying a coarse yellow sandy clay.

The presence of a peat over the mineral soil at an elevation as low as this is noteworthy. Peat was noticed on G. Benom from here to the summit. At camp 4, 5000 ft, it was about 1 ft thick.

The boundary to Lower Montane Rain forest is sharp on G. Benom. With the Lower Montane formation there are local differences in flora. Thus about ¼ mile above camp 3, at about 3800 ft where the ridge swings southwards and becomes narrower, the species composition changes and many of the species one sees on the Main Range, e.g. at Fraser's Hill come in. Prominent in the canopy here due to its velvety brown leaves is the new and beautiful *Palaquium regina-montium* (Sapotaceae), an endemic Malayan species now known from several mountains at about this elevation. The conifer *Dacrydium* comes in, as do *Symingtonia populnea* (Hamamelidaceae) and *Weinmannia blumei* (Cunoniaceae). The giant mountain rattan *Plectocomia griffithii*, was seen only in this zone. From about 4000 ft upwards the tallest forest (canopy about 50 ft) with the biggest trees is on broad ridge-crests and on saddles. Narrow exposed ridges carry low Upper Montane Rain forest with gnarled trees. Lower Montane Rain forest persists on gentle slopes and protected valleys to high elevations. In a broad valley about ¼ mile south-west of camp 4 at about 4800 ft the flora contained several lowland elements, including new altitude records by a few hundred feet in Malaya for *Knema oblongifolia v. monticola* (Myristicaceae) and *Payena lucida* (Sapotaceae). This valley has a grove of the rare Malayan Maple *Acer caesium*. The boundary between Lower and Upper

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* No species list is given, to avoid giving a misleading impression of completeness. Species found at this elevation can be ascertained through appendix 1.

Montane forest, with the former growing high up valleys, is clearly visible on aerial photographs.

Most valley sides and ridge slopes are not gentle, but precipitous and unstable with evidence of land slips. In some places huge boulder piles cover the slopes with caves between and under them. Trees are few and rather small and the undergrowth is very dense with many palm and gingers (Plate 9). Fallen trees are abundant. Many characteristic trees are virtually exclusive to the ridges and do not grow on the unstable boulder littered slopes. Examples are *Ternstroemia* FRI 3320, *Dacrydium comosum* and *D. elatum* and *Podocarpus imbricatus* (Coniferae) and amongst the smaller trees the very lovely pink-flowered *Rhododendron wrayi*.

With increasing elevation one passes through less Lower Montane forest; nearly everywhere is clothed in the Upper Montane formation whose facies and probably species composition varies from place to place, notably with relief.

In places *Baeckia frutescens* (Myrtaceae) and *Leptospermum flavescens* (Myrtaceae) (Plate 10) are abundant. The deep gully at *c.* 6000 ft below and to the south-west of the first peak on the summit ridge has vestiges of Lower Montane forest. It is the last station of the common undergrowth montane palm *Pinanga polymorpha* and of the rattans (a slender *Calamus*).

The first peak, 6760 ft, has an open stunted Upper Montane forest, (Plate 5) almost a pure stand of 15–20 ft *Leptospermum flavescens* (Plate 11) with a little *Dacrydium* over a grassy, bushy undergrowth in which the trunked sedge *Gahnia baniensis* and *Rhododendron obscurum* are conspicuous (Plate 12). Open turfy places carry *Gentiana malayana* (one of the North Temperate—Himalayan plants which reach into Malesia on high mountains), and the small sedges *Lepidosperma chinense* and *Oreobolus kukenthallii*. The ground is covered by thick peat in which the bogmoss *Sphagnum junghunianum* is prominent.

The flora is much less rich than the similar formation on G. Tahan, with which (and probably other high peaks) it shares most of its species.

Upper Montane Rain forest is characterized *inter alia* by abundant epiphytes. These are far less well developed on Benom than is common. Orchids are uncommon. Above *c.* 3500 ft tree boles do have a bryophyte layer but it is only *c.* 1 in. thick. Filmy ferns are inconspicuous. There are no great festoons from the trees even in the moist gullies. The exposed first summit peak has very little bryophyte development indeed.

Slight development of epiphytes and skiophytic climbers as compared with other humid tropical countries seems to be a widespread feature of montane forests of Malaya (see Whitmore & Burnham, 1969, describing G. Ulu Kali in the Main Range). It may reflect the lower rainfall here than elsewhere. G. Benom, lying in the rain shadows of both the Main Range and the east coast mountains, is in a dry part of Malaya and this probably is an important factor limiting the epiphyte flora.

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APPENDIX 1

Previous expeditions to Benom have either been by a botanist or with a botanist, and several species lists have been published with the accounts of the ascents to which Medway has referred in his introduction. Our collections, 408 numbers, are the first from the north-east side of the massif, and in total are probably the biggest made on the mountain.

We do not propose to publish a list of the species collected. They are being named in the normal course of our research work, and duplicates have been distributed to our usual correspondent herbaria: Arnold Arboretum, Kew, Leiden, and Singapore.

We keep a herbarium register at Kepong from which at any time the identities of the plants collected may be ascertained. It is thus sufficient to quote the numbers of the plants which were collected on the mountain, and interested persons can then discover identifications from the register.

FRI	3126–3143	Coll. T. C. Whitmore
FRI	3150–3445	
FRI	3997–4000	
KEP	97801–97850	Coll. Rahim bin Ismail
KEP	99783–	
KEP	100101–100129	
KEP	99101–99150	Coll. Zahir bin Yusof
KEP	104301–104313	Coll. Chelliah
KEP	104382–104450	

Dr. T. C. Whitmore, F.L.S.
Forest Research Institute
Kepong, Malaysia
April, 1968.

THE GUNONG BENOM EXPEDITION 1967

3. BRYOPHYTES AND FILMY FERNS FROM GUNONG BENOM

By ANNE JOHNSON

THE following is a short account of bryophytes and filmy ferns collected on Gunong Benom from 7–9 April 1967. Apart from three collections by J. A. Bullock at 6000 ft, all specimens were collected between 800 and 3800 ft, from the ground, rock surfaces, and lower tree trunks, where possible up to about 6 feet above ground. All specimens have been lodged in the Cryptogamic Herbarium, School of Biological Sciences, University of Malaya. The accession number is given for each collection.

The material confirms to a certain extent Whitmore's general remarks on epiphytes (1972). The extreme poverty of the bryophyte flora in the lowland forest at 800 ft reflects the effect of rain shadow. There is a sharp change in the bryophyte flora at about 2500 ft, especially in valleys. Above this elevation there is a marked increase in both number of species and their abundance, with up to 100% cover in wet places near the ground. There is little distinction between ground and tree bryophytes. Peat found at 3800 ft is not sphagnum peat, but is composed of dead bryophytes other than sphagnum and vascular plant debris. *Sphagnum junghuhnianum* occurs at higher elevations (Whitmore, 1972).

The flora is similar to that of lowland forest and lower montane forest in other parts of Malaya but is noteable for the paucity of members of the Leucobryaceae and Calymperaceae which are far better developed in other areas.

SYSTEMATIC LIST

Dilaenaceae

Pallavicinia indica Schffn. On small stones near the stream, Base camp, 800 ft (B 0964).

Pallavicinia leveiri Schffn. On tree trunks in valley, 2800 ft (B 0950).

Metzgeriaceae

Metzgeria hamata Lindb. On fallen trees in valley, 2800 ft (B 0957).

Riccardiaceae

Riccardia pinguis (L). Gray. In mossy forest, 3800 ft (B 0959).

Riccardia parvula Schffn. On palm inflorescence in valley, 2900 ft (B 0888).

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Jungermaniales Acrogynae

Ptilidiaceae

Trichocolea tomentella Huds. On ground, Base camp, 800 ft (B 0902).

Cephaloziellaceae

Cephaloziella sp. Abundant, in mossy forest, 3800 ft (B 0923, B 0939, B 0940, B 0941).

Bazzaniaceae

Bazzania distans (Nees.) Trev. With seedlings of *Podocarpus*, 6000 ft, collected by J. A. Bullock (B 0899).

Bazzania longicaulis (Lac.) Schffn. In mossy forest, 3800 ft (B 0916, B 0929).

Lejeuneaceae

Schistochila sp. In mossy forest, 3800 ft (B 0923, B 0927, B 0956).

Stictolejeunea sp. At Base camp, 800 ft (B 0962).

Musci

Dicranaceae

Dicranoloma blumii (Nees.) Par. In mossy forest, 3800 ft (B 0915).

Leucobryaceae

Leucobryum candidum (P. Beauv.) Wils. In mossy forest, 3800 ft (B 0912, B 0955).

Leucophanes octoblepharoides Brid. On trees at Base camp, 800 ft (B 0984); in valley, 2800 ft (B 0890, B 0896).

Syrrhopodontaceae

Syrrhopodon croceus Mitt. In mossy forest, 3800 ft (B 0924).

Syrrhopodon schiffnerianus (Fleisch.) Par. In mossy forest, 3800 ft (B 0931, B 0945).

Syrrhopodon spiculosus Hook. at Grev. In mossy forest, 3800 ft (B 0887, B 0910, B 0914, B 0922, B 0928, B 0958).

Syrrhopodon treubii Fleisch. In valley, 2800 ft (B 0893, B 0898); in mossy forest, 3800 ft (B 0921).

Thyridium undulatum (Broth. et Geh.) Fleisch. In valley, hanging from the trees, 2800 ft (B 0889).

Calymperaceae

Calymperes hampei Doz. et Molk. On trees, Base camp, 800 ft. (B 0889).

Calymperes longifolium Mitt. In isolated patches on trees in the valley, 2800 ft (B 0909).

Orthotrichaceae

Groutiella goniorrhyncha (Doz. et Molk.) Wijk. et Marj. On trees at Base camp, 800 ft (B 0906).

Rhizogoniaceae

Rhizogonium spiniforme (Hedw.) Bruch. On ground in valley, 800 ft (B 0946).

Meteoriaceae

Aerobryopsis longissima (Doz. et Molk.) Fleisch. In valley, 2800 ft (B 0901); in mossy forest, 3800 ft (B 0933).

Neckeraceae

Thamnium ellipticum (v.d.B. et Lac.) Kindb. On tree trunks at Base camp, 800 ft (B 0984).

Thuidiaceae

Thuidium meyenianum (Hpe.) v.b.B. In the valley, 2800 ft (B 0895).

Hookeriaceae

Callicostella pappillata (Mont.) Mitt. On tree bark, Base camp, 800 ft (B 0911); valley on trees, 2800 ft (B 0952).

Distichophyllum mittenii Bosch. et Lac. In mossy forest, 3800 ft (B 0944).

Sematophyllaceae

Clastobryophilum bogoricum (Bosch. et Lac.) Fleisch. Very abundant in mossy forest, 3800 ft (B 0947, B 0951, B 0953, B 0966).

Acroporium diminutum (Brid.) Fleisch. On trees in the valley, 2800 ft (B 0892).

Sematophyllum saproxylopilum (C. Muell.) Fleisch. In the valley, 2800 ft (B 0897).

Trichosteleum mammosum (C. Muell.) Jaeg. In the valley, 2800 ft (B 0961).

Trismegista lancifolia (Harv.) Broth. In mossy forest, 3800 ft (B 0886, B 0930, B 0935).

Hypnaceae

Ectropothecium intorquatum (Doz. et Molk.) Jaeg. In the valley, 2800 ft (B 0963).

Hypnodendraceae

Hypnodendron reinwardtii (Reinw. et Hornsch.) Lindb. In mossy forest, 3800 ft (B 0919, B 0954, B 0960).

Filicinae

Hymenophyllaceae

Hymenophyllum acanthoides (v.d.B.) Rosenst. In peaty area, 6000 ft, collected by J. A. Bullock (B 0903).

Trichomanes meifolium Bory. On exposed slope, 6000 ft, collected by J. A. Bullock (B 0900).

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Professor Anne Johnson
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Singapore 22

B

Photographs by Lord Medway

PLATE 1

A fine tualang (*Koompassia excelsa*), temporarily deciduous, standing alongside the track to Base camp.

B*

PLATE 2

A disused extraction track at 1000 ft. Note the height of standing timber (compare the figure of a man, arrowed), and the dense thickets of young vegetation springing up on both sides.

PLATE 3

The track to camp 2, at 1600 ft, running among relatively undisturbed forest vegetation. The vertical scale is indicated by the figure of a man (arrowed).

PLATE 4

Lower Montane Rain forest near camp 3.

PLATE 5

Ridge vegetation at 4700 ft. Note the figure of a man (arrowed).

PLATE 6

Blossoms of *Leptospermum flavescens*, photographed near the summit of Benom.

PLATE 7

A stand of *Leptospermum flavescens* on the north-east end of the summit ridge, at 6760 ft.

PLATE 8

The undergrowth of sedge and low bushes between *Leptospermum* trees at 6760 ft.

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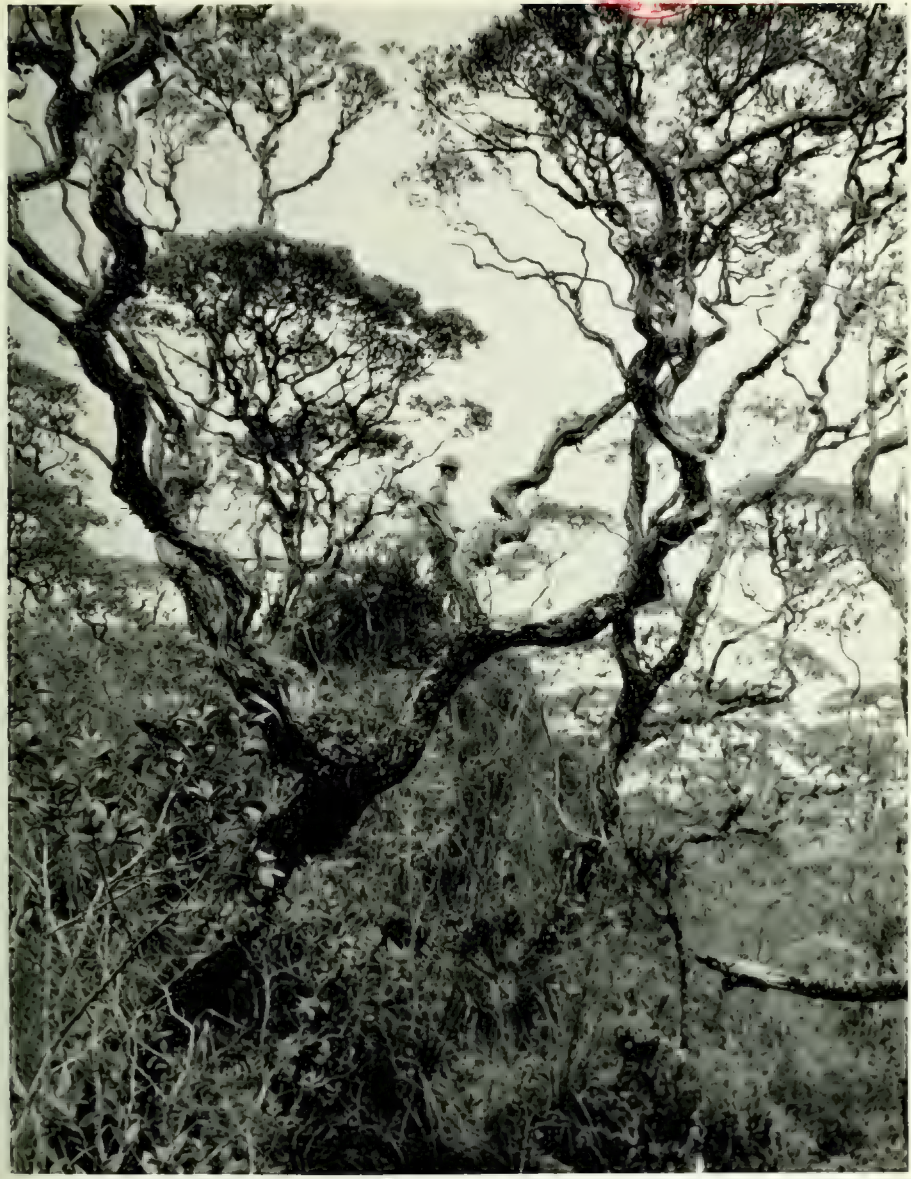

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THE GUNONG BENOM EXPEDITION 1967

4. NEW RECORDS OF MALAYAN BATS, WITH TAXONOMIC NOTES AND THE DESCRIPTION OF A NEW *PIPISTRELLUS*

J. E. HILL

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THE GUNONG BENOM EXPEDITION 1967

4. NEW RECORDS OF MALAYAN BATS, WITH TAXONOMIC NOTES AND THE DESCRIPTION OF A NEW *PIPISTRELLUS*

By J. E. HILL

THE 1967 Expedition to Gunong Benom, Pahang, 1965 resulted in the accession of a number of specimens of bats of especial taxonomic interest, including one example that has proved to represent an undescribed species of *Pipistrellus*. Additionally, during recent years, specimens of similar interest or in some cases representing species new to Malaya have been received from Lord Medway, formerly of the Unit of Zoology, School of Biological Sciences, at the University of Malaya, Kuala Lumpur.

All measurements in this paper are in millimetres : where these refer to a series of specimens the minimum and maximum values are given, followed by the mean in parentheses.

Rhinolophus malayanus Bonhote, 1903

♀ B.M. 68.812 (in alcohol, skull extracted). Wang Tangga, Kaki Bukit, Perlis, 6° 39′ N, 100° 12′ E. 2 January 1968.

♂ B.M. 68.816, ♀♀ B.M. 68.813–815 (all in alcohol, skulls extracted). Kisap Forest Reserve, Pulau Langkawi, Kedah, 6° 23′ N, 99° 52′ E. 31 December 1967.

Rhinolophus malayanus is not listed from the States of Malaya by Chasen (1940 : 36) and does not appear to have been subsequently recorded. Described originally from Biserat, Patani, southern Thailand, its presence in Perlis and on Pulau Langkawi is not unexpected. The species is recorded from Koh Lak, on the east coast of southern Thailand rather to the north of Patani by Gyldenstolpe (1916 : 13), from the Laos Mountains by Andersen (1905a : 89) and from Laos by Tate and Archbold (1939 : 6) and by Phillips (1967 : 634), while Osgood (1932 : 218) records it provisionally from Muong Moun, Tonkin (North Vietnam).

These specimens from Perlis and Langkawi agree closely with the type specimen, having the lancet with slightly concave lateral margins and an elongate tip and with the lateral margins of the sella almost parallel. The connecting process is rounded and rises slightly above the tip of the sella: its point of insertion on the posterior leaf is a little above the corresponding insertion on the back of the sella. The small anterior premolar (pm^2) is in the toothrow but much reduced: the second lower premolar (pm_3) is slightly extruded or is external to the toothrow, with pm_2 and pm_4 sometimes almost in contact.

MEASUREMENTS (B.M. 68.812, 68.816, 68.813–815, in that order): length of forearm 40·3, 39·6, 42·2, 41·2, 40·7; width of sella, 2·2, 2·0, 2·1, 2·0, 1·9; greatest length of skull 18·2, 18·5, 18·0, 17·9, 18·0; condylocanine length 15·3, 15·5, 15·2, 15·2, 15·1; supraorbital length (distance from junction of supraorbital ridges to median anterior point of nasal swellings) —, 4·9, 4·9, —, 4·8; width of nasal swellings —, 4·9, 5·1, 5·1, 5·0; zygomatic width 8·8, 8·9, 8·8, 8·5, 8·8; least interorbital width —, 2·2, 2·3, 2·3, 2·4, width of braincase 7·4, 7·4, 7·4, 7·4, 7·4; mastoid width 8·4, 8·4, 8·2, 8·3, 8·3; c^1–c^1 4·4, 4·5, 4·4, 4·2, 4·3; m^3–m^3 6·7, 6·5, 6·5, 6·4, 6·3; c–m^3 6·8, 6·8, 6·6, 6·5, 6·6; length of mandible 11·3, —, —, —, 11·4; c—m_3 6·9, 7·2, 6·9, 6·8, 6·8.

Rhinolophus malayanus is very similar to *R. borneensis*, differing chiefly in the size and shape of the median anterior nasal swellings, which in *malayanus* are more inflated, higher, wider and more clearly demarcated than in *borneensis*, extending laterally down the sides of the rostrum and thereby reducing the area of the lateral swellings as compared with that species. Robinson and Kloss (1915 : 116) recorded as *R. borneensis* (?) a specimen from Khao Nawng, Bandon, southern Thailand but this subsequently became the type specimen of *R. robinsoni* Andersen (1918 : 375). An examination of the type specimen of *R. chaseni* Sanborn (1939 : 38) from Con Son Island (Pulo Condore), off the southeast coast of Indochina indicates that *chaseni* should be considered a subspecies of *R. borneensis* rather than related to *R. malayanus* as was suggested by its describer or conspecific with it as thought by Phillips (1967 : 634) from the published description.

Rhinolophus robinsoni Andersen, 1918

A single specimen from Fraser's Hill, Pahang (see below) resembles the nominal species *robinsoni* and *klossi* in its major features and although in some respects it differs slightly from these, in others it connects them. They have never been described in detail and rest on brief diagnoses by Andersen in a key published (on behalf of Andersen by Oldfield Thomas) in 1918. The examination of a limited number of specimens suggests that they are conspecific: *robinsoni* has line priority and becomes the specific name.

The species is relatively small with large, bluntly pointed ears; prominent antitragal lobe; large anterior leaf covering the muzzle; lancet cuneate; sella wide, its central part (excluding the basal lobes) expanded laterally so that its width at this point nearly equals or is greater than the width at its base, but sharply constricted a little above its central point; upper margin of sella slightly convex; connecting process low and rounded, its insertion on the posterior leaf level with or beneath its insertion on the back of the sella; third, fourth and fifth metacarpals subequal; second phalanx of third digit short, its length less than one and one half times the length of the first phalanx; braincase elongate with low sagittal crest; supraorbital region relatively long, the supraorbital length (from junction of supraorbital crests to median anterior point of nasal swellings) exceeding the width across the lateral anterior nasal swellings; a clearly defined frontal depression; prominent nasal swellings, the median anterior pair high and globular; mesopterygoid fossa wide with deep mesopterygoid pit; anterior upper premolar (pm^2) in the toothrow, usually in contact with canine and posterior premolar (pm^4); second lower premolar (pm_3) small, partially or wholly extruded, with pm_2 and pm_4 sometimes in contact or nearly so. Measurements appear in Tables 1 and 2.

The external and cranial features of *R. robinsoni* refer it to the *ferrumequinum* group of Tate and Archbold (1939 : 2) (the *simplex* group of Andersen (1905a : 75, 1905b : 648) or *megaphyllus* group of that author (1918 : 374). Its wing structure places it in either the *simplex* (more properly the *megaphyllus*) or *borneensis* subgroups of Tate and Archbold[1] and not in the *affinis* subgroup as these authors defined it and in which they listed both *robinsoni* and *klossi*. The long supraorbital region of *robinsoni* is characteristic of the *simplex* subgroup but its rounded sella, short palatal bridge and extruded second lower premolar ally it more closely to the *borneensis* subgroup and the species is evidently closely related to *R. borneensis* which in many respects it resembles. However, in *R. borneensis* the sella is narrower with its lateral margins parallel or nearly so and the connecting process is inserted on the posterior leaf at a point above its insertion on the back of the sella. The supraorbital region is shorter and the median anterior nasal swellings in *borneensis* less globular and wider, extending laterally to the sides of the rostrum.

Rhinolophus robinsoni robinsoni Andersen, 1918

Rh[*inolophus*] *robinsoni* Andersen, 1918 : 375. Khao Nawng, Bandon, Lower Thailand. Type specimen B.M. 18.8.2.1 (in alcohol (in bad condition), skull extracted).

Larger than *R.r. klossi* with slightly narrower lancet; width of sella as in *klossi*, not greater as stated by Andersen; palate wider; mesopterygoid fossa wider anteriorly; sphenoidal bridge very slightly wider; second lower premolar (pm_3) completely extruded with pm_2 and pm_4 in contact.

Rhinolophus robinsoni klossi Andersen, 1918

Rh[*inolophus*] *klossi* Andersen, 1918 : 375. Pulau Pemanggil, Johore Archipelago, off east coast of Malaya. Type specimen B.M. 18.8.5.5 (in alcohol, skull extracted). June 1915.

(?) ♂ B.M. 67.214 (in alcohol, skull extracted). Pine Tree Hill, Fraser's Hill, Pahang, 3° 43′ N, 101° 42′ E, at 4500 ft. 10 October 1966.

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[1] Tate and Archbold mistakenly noted (p. 5) that the second phalanx of the third digit is unshortened in the *simplex* and *borneensis* subgroups and shortened in the *affinis* and *ferrumequinum* subgroups: in fact, the reverse is true as indicated by Andersen (1905a).

Smaller than *R.r. robinsoni* with lancet slightly wider at its base; palate narrower; mesopterygoid fossa narrower anteriorly; sphenoidal bridge narrower; second premolar (pm_3) partially or wholly extruded, pm_2 and pm_4 separated by a narrow space or in contact. One example (B.M. 55.1479, from Pulau Pemanggil) has the right pm_3 completely extruded but the left pm_2 has been lost and pm_3 in this ramus remains wholly in the toothrow. Specimens from Pulau Pemanggil and Pulau Aor have relatively small skulls: one specimen from Pulau Tioman has a slightly longer forearm and a larger skull approaching the skull of *robinsoni* in size but nevertheless this example retains the narrow palate, narrow mesopterygoid fossa and narrow sphenoidal bridge of *klossi*.

The specimen from Pahang is referred to *klossi* with some reservation. Externally, it almost exactly resembles this subspecies, but although its skull is similar to that of *klossi*, in size it approaches or in some respects exceeds the skull of *robinsoni* and the supraorbital region is longer and the mesopterygoid fossa narrower than in either of these. The material available, however, is totally inadequate for any attempt at evaluating the status of the northern and southern populations of *R. robinsoni* on the Malay Peninsula.

TABLE I

EXTERNAL MEASUREMENTS OF *Rhinolophus robinsoni*

		R.r. klossi					
	R.r. robinsoni B.M. 18.8.2.1. Type Southern Thailand	B.M. 18.8.5.5. Type Pulau Pemanggil	B.M. 61.1709 Pulau Pemanggil	B.M. 61.1710 Pulau Pemanggil	B.M. 61.1711 Pulau Aor	B.M. 61.1712 Pulau Tioman	*R.r.* (?) *klossi* B.M. 67.214 Malaya
Length of forearm	45·3	41·8	40·9	—	42·2	43·6	41·8
IIIrd. metacarpal	34·0	31·3	30·6	31·1	31·0	32·8	31·3
III^1	14·5	12·8	12·3	13·7	12·8	13·3	12·7
III^2	19·7	17·6	16·8	18·3	18·1	19·1	18·3
IVth. metacarpal	33·8	32·0	—	33·1	32·1	34·1	32·9
IV^1	11·4	9·5	9·2	10·0	9·3	10·3	9·5
IV^2	12·1	10·3	10·1	11·3	11·4	11·5	11·2
Vth. metacarpal	33·8	31·8	31·1	32·1	32·2	34·2	32·0
V^1	11·5	10·0	9·8	10·7	9·7	10·4	9·8
V^2	12·5	10·8	10·2	11·3	10·9	11·2	11·4
Width of sella	2·7	2·5	2·8	2·7	3·0	2·9	2·8
Length of tibia	19·4	16·8	16·3	16·8	17·5	17·6	18·3

TABLE 2

CRANIAL MEASUREMENTS OF *Rhinolophus robinsoni*

		R.r. klossi					
	R.r. robinsoni B.M. 18.8.2.1. Type Southern Thailand	B.M. 18.8.5.5 Type Pulau Pemanggil	B.M. 55.1479 Pulau Pemanggil	B.M. 55.1480 Pulau Pemanggil	B.M. 61.1711 Pulau Aor	B.M. 61.1712 Pulau Tioman	*R.r.* (?) *klossi* B.M. 67.214 Malaya
Greatest length of skull	—	—	—	18·2	18·0	19·8	20·3
Greatest length of skull to canine	19·2	—	—	18·0	17·5	19·0	19·2
Condylocanine length	17·2	—	—	16·0	15·5	16·9	17·0
Length of palatal bridge	2·0	2·0	2·0	2·0	1·8	2·1	2·1
Supraorbital length	5·3	5·2	5·1	5·3	5·2	5·5	6·0
Width of nasal swellings	5·2	5·0	4·9	5·0	5·0	5·2	5·5
Zygomatic width	9·7	9·3	9·2	9·4	9·1	9·5	9·7
Least interorbital width	2·6	2·5	2·4	2·3	2·6	2·5	2·6
Width of braincase	—	—	—	—	7·4	7·9	8·4
Mastoid width	9·2	—	—	—	8·5	8·9	9·2
Width of mesopterygoid fossa	3·2	2·8	2·8	2·9	2·9	2·9	2·7
Width of sphenoidal bridge	1·7	1·5	1·4	1·5	1·4	1·4	1·5
c^1–c^1	4·6	4·5	4·4	4·6	4·3	4·4	4·6
m^3–m^3	6·9	6·5	6·5	6·6	6·4	6·6	6·8
c–m^3	7·2	6·8	6·6	6·8	6·6	7·2	7·3
Length of mandible	12·5	—	11·5	—	—	12·3	12·8
c–m_3	7·6	7·3	7·1	7·3	7·0	7·6	7·8

Rhinolophus macrotis dohrni Andersen, 1907

♂ B.M. 67.1595 (in alcohol, skull extracted), ♀ B.M. 67.1596 (skin and skull). Base Camp, Gunong Benom, Pahang, 3° 51′ N, 102° 11′ E, 700 ft. 20–23 February 1967.

♂ B.M. 67.1597 (in alcohol). Above Camp 2, Gunong Benom, 2500 ft. 7 April 1967.

♂♂ B.M. 67.1598–1598A (in alcohol). Camp 3, Gunong Benom, 3500 ft. 7–8 March 1967.

♂♂ PM 45, PM 47–48 (skeletons), B.M. 67.1599 (in alcohol), PM 43 (in alcohol, returned to the University of Malaya). Camp 3, Gunong Benom, 3600 ft. 10–11 March 1967.

Rhinolophus macrotis has not previously been recorded from the States of Malaya although known from Sumatra (*R.m. dohrni*) and, following Tate (1943 : 2), from Thailand (*R.m. siamensis*), Fukien (*R.m. caldwelli*), Szechuan (*R.m. episcopus*), Nepal (*R.m. macrotis*) to the Philippines. However, according to Osgood (1932 : 219), *caldwelli* and *siamensis* are apparently sympatric in Tonkin (North Vietnam) but the specimens he refers to *siamensis* are intermediate in size between *caldwelli* and the very much smaller *siamensis*. Specimens from Gunong Benom agree very closely with *R.m. dohrni* but are very slightly larger: among Malayan *Rhinolophus* the species may be readily recognized by its cuneate lancet, very broad, tongue-shaped sella which has a light covering of hairs on its anterior face, and low connecting process which originates below the apex of the sella. Cranially it is distinguished by its long palatal bridge and by the anterior upper premolar (pm^2), which has a prominent, inwardly deflected cusp and which stands in the toothrow and is divided from the canine and posterior premolar (pm^4) by small interspaces.

Measurements of seven specimens in alcohol and five skulls (except where stated): length of forearm 44·5–45·3 (44·9); greatest length of skull 19·1–19·5 (19·4); greatest length of skull to front of canine 18·5–18·7 (18·6); condylocanine length 16·3–16·7 (16·5); basilar length to front of canine 14·6 14·9 (14·8); width of nasal swellings 5·0–5·2 (5·1); zygomatic width 8·3–8·6 (8·5); least interorbital width (four skulls 2·4 2·6 (2·5); width of braincase 7·5–7·8 (7·6); mastoid width 8·8—9·2 (8·9); c^1–c^1 4·0–4·3 (4·1); m^3-m^3 5·7–5·9 (5·8); c m^3 6·6–6·8 (6·7); length of mandible (two skulls) 11·8; c–m$_3$ 6·8–7·0 (6·9).

Hipposideros lylei Thomas, 1913

♂♀ B.M. 64.831 832 (in alcohol, skulls extracted). Wang Tangga, Kaki Bukit, Perlis, 6° 39′ N, 100° 12′ E. 7 March 1964.

Chasen (1940 : 42) listed *H. lylei* from the States of Malay, apparently on the basis of two skins in the collection of the National Museum, Singapore from Bukit Chintamani, Pahang (Medway, in litt.). Described originally from Thailand, its occurrence in the northern part of the States of Malaya is not unexpected. Measurements (B.M. 64.831-832): length of forearm 78·2, 75·0 greatest length of skull 30·2, 29·0; condylobasal length 26·8, 25·5; condylocanine length 26·3, 25·3; rostral width 9·4, 9·3; zygomatic width 15·9, 15·9; least interorbital width 4·4, 4·2; width of braincase 12·0, 11·9; mastoid width 14·2, 14·1; c^1–c^1 7·3, 7·1; m^3–m^3 11·0, 10·7; c–m^3 11·3, 11·0; length of mandible 19·9, 18·9; c–m$_3$ 12·4, 12·0.

Coelops frithii Blyth, 1848

♂ B.M. 67.215 (in alcohol, skull extracted but fragmentary). 16th. mile, Ulu Gombak, Selangor, 3° 18′ N, 101° 43′ E. 27 October 1966.

This specimen constitutes the first definitive record of the species from the States of Malaya. Bats of the genus *Coelops* are rare in collections and its taxonomy seems uncertain: Tate (1941a : 5) reviewed it briefly and summarized its history but no subsequent work has appeared. The discovery of *C. frithii* in Malaya has led to an examination of the material of *Coelops* in the collections of the British Museum (Natural History), which, although quite inadequate for any general revisionary treatment, has sufficed to show that two distinct species exist in that country and which has suggested the likely allocation of most of the remaining named forms.

The Malayan specimen agrees closely with *C. frithii* which may be characterized by: elongate, narrow outline of the lappets projecting from the supplementary leaflets flanking the anterior leaf; narial part of the anterior leaf not especially depressed and not sharply demarcated from the intermediate part of the leaf, the intervening ridges extending from the central process or 'sella' toward the lateral margins of the leaf low and indefinite; posterior part of the upper surface of the rostrum sloping anteriorly; rostral inflations low, separated by a shallow sulcus, in profile forming only a slight convexity; a definite pocket or recess within the maxillary root of the zygoma, the upper edge of which is shallowly curved anteriorly to terminate on the rostrum above the anterior face of the second molar; upper toothrows convergent anteriorly; posterior lower premolar (pm_4) elongate and narrow; lower molars with prominent, horizontal external cingula. Named forms apparently conspecific with *frithii* are *bernsteini* Peters, *inflatus* Miller, *sinicus* G.M. Allen, and *formosanus* Horikawa. The range of the species extends from Bengal (*frithii*) to southern China (*sinicus, inflatus*), Formosa (*formosanus*) to Java and Bali (*bernsteini*: Tate (1941a : 7, 11) records specimens from Bali). Osgood (1932 : 226) records *inflatus* from Tonkin and Annam (North Vietnam) and there are specimens from Laos and Thailand in the British Museum (Natural History) which must be referred to *C. frithii*, previously recorded from Thailand by Gyldenstolpe (1916 : 15). The Malayan example thus fills a distributional hiatus but insufficient specimens are available to justify any attempt at elucidating the validity of subspecies or to allocate it at this level. Measurements of this specimen : length of forearm 43·8; of tibia 17·0; maxillary toothrow (c–m^3) 5·7.

The type specimen of *C. robinsoni* Bonhote (1908 : 4) from the foot of Gunong Tahan, Pahang differs so markedly from *C. frithii* as to justify specific separation although Ellerman and Morrison-Scott (1951 : 132) considered the possibility that these might be conspecific. *Coelops robinsoni* may be distinguished from *C. frithii* by: rounded, wide outline of the lappets projecting from the supplementary leaflets; narial part of the leaf depressed and sharply demarcated from the intermediate leaf by prominent ridges extending from the central process or 'sella' toward the lateral margins of the leaf; posterior part of the upper surface of the rostrum nearly horizontal and only slightly inclined anteriorly; rostral elevations large, separated by a prominent sulcus, in profile forming a distinct convexity; a small foramen but no definite pocket or recess within the maxillary root of the zygoma, the upper edge of which is sharply curved anteriorly to terminate on the rostrum above the posterior face of the second molar; upper toothrows nearly parallel; posterior lower premolar (pm_4) wide; lower molars with low, upwardly curving cingula.

The genus *Chilophylla* was described by Miller (1910 : 395) for the species *Chilophylla hirsuta*, described concurrently from the Alag River, Mindoro, Philippines, from a skin without skull. Later, this author (1912 : 117) referred a specimen

(United states National Museum 175000) from Port Swettenham, Malaya to *hirsuta* and described the cranial characters of the species from its skull. Subsequently, Miller (1928 : 85) agreed with an opinion originally advanced by Andersen (in litt.) that *Chilophylla* should be referred to the synonymy of *Coelops*, but the name has nevertheless persisted, Taylor (1934 : 247) using it in his account of the Philippine land mammals and Chasen (1940 : 48) including it in the Malaysian fauna, admittedly with the reservation that it seemed extremely close to *Coelops*. There can be no doubt from the meticulous descriptions of the skull of U.S.N.M. 175000 by Miller (1912 : 117) and Tate (1941a : 5) together with the plate in Howell (1929 : pl. 2, fig. 2e) which presumably depicts this skull (as *C. robinsoni*) that this specimen from Port Swettenham represents *C. robinsoni*. The status of *C. hirsuta* must remain uncertain until the features of its skull are known but its small size (length of forearm 33·8), the presence of a curved ridge extending laterally above each nostril towards the margin of the horseshoe and the statement by Miller (ibid.) that he could detect no external peculiarities that seemed of specific importance between *hirsuta* and the Port Swettenham specimen suggest affinity with *C. robinsoni*.

Coelops robinsoni is recorded from Teratau Island, Thailand by Chasen (1940 : 47) and from Khao Nawng, Bandon, southern Thailand by Robinson and Kloss (1915 : 116). The two specimens recorded by Robinson and Kloss are now in the British Museum (Natural History) (B.M. 68.605–606, formerly Federated Malay States Museum 531/12, 532/12): both are subadult and their skulls cannot now be found. From their external features both are referable to *C. frithii*, the length of the forearm in B.M. 68.605 being 39·4 and in B.M. 68.606 38·2 while the measurements of the skulls as quoted by Robinson and Kloss are in close agreement with those of that species.

Myotis siligorensis (Horsfield, 1855)

♂ B.M. 67.219 (skin and skull). Cheras cave, Panching, near Kuantan, Pahang, 3° 53′ N, 103° 09′ E. 23 January 1967.

This is the first record of *Myotis siligorensis* from the States of Malaya. Although there are few specimens in collections the species has been recorded from Kumaon, Nepal and Sikkim (*M.s. siligorensis*), Fukien (*M.s. sowerbyi* Howell), Tonkin (North Vietnam) (*M.s. alticraniatus* Osgood) and Thailand (*M.s. thainus* Shamel). From descriptions this specimen is similar to *alticraniatus* or *thaianus* but in the absence of comparative material no definitive subspecific determination can be made. The dorsal surface of the specimen is dark brown and the ventral surface of similar colour but slightly more buffy. Measurements: length of forearm (from collector) 29·6; greatest length of skull 12·2; condylobasal length 11·1; condylocanine length 10·4; zygomatic width 7·0; least interorbital width 3·0; width of braincase 6·0; depth of braincase 4·5; mastoid width 6·3; m^3–m^3 4·6; length of entire upper toothrow 5·1; c–m^3 4·4. Bats of this species may be recognized by their small size, high, domed braincase and much reduced canines, the lower tooth about equal in height to the posterior lower premolar (pm_4), with the second lower premolar (pm_3) in the axis of the toothrow.

Myotis horsfieldii horsfieldii (Temminck, 1840)

♂♂ B.M. 65.320 (skin and skull), B.M. 65.321 (in alcohol, skull extracted). Ampang Reservoir, Kuala Lumpur, Selangor 3° 11′ N, 101° 49′ E. 15 October 1964.

Vespertilio horsfieldii Temminck was considered a synonym of *Myotis adversus* (Horsfield, 1824) by Dobson (1878 : 291 et seq) and by Tate (1941b : 551, 558). However, Thomas (1910 : 385) identified a series of specimens from Java (which he (with Wroughton) had formerly (1909a : 381) determnied as *M. hasseltii*) as *M. horsfieldii*, pointing out that this species could be distinguished from *M. adversus* by the attachment of the wing membrane to the metatarsus instead of to the end of the tibia as in *adversus*. It is clear from a drawing now preserved in the British Museum (Natural History) copy of Monographies de Mammalogie at Temminck's description of *horsfieldii* that Thomas had submitted illustrations of this feature in his "*adversus*" from Java and in the specimens of "*hasseltii*" which he had from the same collection to F. A. Jentink at the Rijksmuseum van Natuurlijke Historie, Leiden, wherein are Temminck's type specimens. Jentink indicates on this drawing that the insertion of the wing membrane in one of the "cotypes" of *horsfieldii* ('c' of his catalogues (1887 : 280, 1888 : 186)) is identical with the specimens which Thomas considered representative of *hasseltii* and which he subsequently recognised as *horsfieldii*.

Myotis horsfieldii is a relatively small species, the dorsal surface being blackish and the ventral surface blackish grey, with narrow, uninflated braincase, narrow interorbital region, interdental palate terminating anteriorly to a line joining the posterior faces of m^{3-3}, long post-palatal extension, the median post-palatal spine supported by bony laminae. The second upper premolar (pm^3) is large, one quarter to one third the crown area of pm^2, usually but not always completely intruded from the toothrow so that pm^2 and pm^4 are almost in contact, with pm^2 not compressed in the row; second lower premolar (pm_3) one third or a little more the crown area of pm_2, separating pm_2 and pm_4 but usually slightly intruded from the toothrow. The species may be distinguished from *M. adversus* and *M. hasseltii* by its small size, blackish coloration and narrow braincase. These specimens (and one other, ♀ B.M. 62.2133, also from Ampang Reservoir, obtained originally by the Institute for Medical Research, Kuala Lumpur) agree closely with *M.h. horsfieldii* and are rather larger than *M. deignani* Shamel, 1942, from Chiengmai, Thailand, which seems likely to be a subspecies of *M. horsfieldii*.

Measurements (B.M. 65.320–321, 62.2133 (forearm only), in that order): length of forearm 38·7, 37·8, 36·4, 36·9; greatest length of skull 15·7, 15·9, 15·2; condylobasal length 14·3, 14·2, 13·7; condylocanine length 13·6, 13·6, 13·1; zygomatic width —, 9·3, —; least interorbital width 3·6, 3·5, 3·4; width of braincase 7·3, 7·3, 6·9; mastoid width 7·9, 7·9, 7·5; c^1–c^1 4·3, 4·2, —; m^3–m^3 6·1, 6·1, 5·7; c–m^3 5·7, 5·9, 5·6.

Myotis hasseltii (Temminck, 1840)

♀ B.M. 65.322 (skin and skull). Kuala Gula, Perak, 4° 52′ N, 100° 32′ E. 8 November 1964.

♂ B.M. 68.842, ♀ B.M. 68.843 (both in alcohol, skulls extracted). Kuah, Pulau Langkawi, Kedah 6° 16′ N, 99° 50′ E. 1 January 1968.

♀ subadult B.M. 68.844 (in alcohol). Kangar, Perlis, 6° 27′ N, 100° 12′ E. 1 January 1968.

These specimens agree closely with those from Lekop, Karimon Island, Riau Archipelago, Indonesia recorded by Thomas and Wroughton (1909b : 110) as '*Myotis adversus* (Horsf.) (?)' and subsequently identified by Thomas (1916 : 4) as *Leuconoe hasseltii*, and also with two specimens from Java labelled as originating from the Rijksmuseum van Natuurlijke Historie, Leiden prior to 1844 and thereby possibly examined by Temminck. They may be distinguished from specimens attributed to the otherwise similar species *adversus* by their short and not woolly pelage, short post-palatal extension lacking thin bony laminae supporting the post-palatal spine and in having a minute second upper premolar (pm^3) with the second lower premolar (pm_3) very small, usually intruded from the toothrow sometimes to the extent that pm_2 and pm_4 are in contact. There exist apparently two colour variants: two specimens from Java (both old) are brownish above and below as is one from Karimon Island but two others from that island and four from Malaya are greyish brown dorsally and paler greyish white or greyish buff ventrally.

MEASUREMENTS (B.M. 65.322, B.M. 68.842–843); length of forearm 40·2, 40·7, 41·2; length of foot 8·5, 10.0, 9·5; greatest length of skull —, 16·3, 16·1; condylobasal length 14·2, 15·0, 14·8; condylocanine length 13·5, 14·3, 14·0; zygomatic width —, 10·3, —, least interorbital width 3·8, 4·2, 3·9; width of braincase 7·6, 8·0, 8.0; mastoid width 8·0, 8·7, 8·6; c^1–c^1 4·1, 4·6, 4·5; m^3-m^3 6·1, 6·6, 6·6; c–m^3 5·7, 6·1, 6·0.

The named forms of large-footed *Myotis* (sometimes referred to a subgenus, *Leuconoe*) from southeastern Asia need detailed revision but unfortunately the majority seem represented by no more than a few isolated specimens or by a series from no more than one or a few localities. There seems little doubt that *horsfieldii* is a distinct species (Medway, 1965 : 60) despite the views of Dobson (1876 : 127, 1878 : 292) and Tate (1941b : 551, 598) that it is a synonym of *adversus*. The relationship between *hasseltii* and *adversus* as here understood is obscure and it may be that the advent of further Javan specimens and an examination of the type material in Leiden might well alter their taxonomy. Meanwhile, *hasseltii* is used for those bats in which pm_3 is very small and usually intruded or fully intruded from the toothrow, *adversus* for those in which this tooth is larger and stands within the toothrow or is only slightly intruded, and which have rather long, woolly pelage and a long post-palatal extension, its median spine supported by thin bony laminae.

Pipistrellus javanicus javanicus (Gray, 1838)

♂ (skin and skull) B.M. 71.813). Camp 2, Gunong Benom, Pahang 3° 51′ N, 100° 11′ E, 1700 ft. 31 January 1968.

The small anterior upper premolar is sometimes lacking from the toothrows of *Pipistrellus* (Kuzyakin, 1944 : 101, 1950 : 338 et seq., 1965 : 103); on the other hand, it may sometimes be present in those of *Eptesicus* (Hayman, 1954 : 289, 290; Hill, 1966 : 303). However, this specimen is noteworthy for the presence of a small supernumerary premolar in the right toothrow, situated internally in a shallow angle formed by the postero-internal face of the canine and the antero-internal face of the anterior upper premolar normal to this species, which is situated more nearly in the line of the toothrow than the corresponding tooth in the other row. The supernumerary tooth is small, with a narrow cingulum and a slender conical cusp slightly exceeding the normal anterior premolar in height and just visible externally. It is tightly in contact with the canine and the normal anterior premolar, with a basal area of one half that of this tooth. There are no pecularities in the mandibular dentition.

Pipistrellus ridleyi Thomas, 1898[1]

♂ B.M. 67.1604 (skin and skull). Base Camp, Gunong Benom, Pahang, 3° 51′ N, 102° 11′ E, 700 ft. 16 February 1967.

This species has been represented hitherto in the collections of the British Museum (Natural History) only by the type and paratype specimens, B.M. 98.3.15.5–6, from Selangor. The teeth of the example from Gunong Benom are less worn than are those of the type specimen and agree closely with those of the paratype, the skull of which has now been prepared from the specimen in alcohol. The description of the incisors by Thomas is based solely on the type specimen and an examination of specimens in which wear is less evident enables some additional features to be noted. The inner upper incisor (i^2) is low, short and wide, narrow anteriorly but wider posteriorly, its length at the cingulum only slightly exceeding its greatest width. The principal cusp is projected forward beyond the premaxilla and is directed slightly inwardly rather than anteriorly: in profile its anterior surface is strongly convex and its posterior face slightly concave so that it is hooked posteriorly. There are low, paired posterior accessory cusps; the labial cusp is smaller than the lingual cusp and in the type specimen is almost worn away so that the inner cusp becomes readily visible from the side. The outer upper incisor (i^3) is short and wide, its width exceeding its length, and has a principal cusp hooked posteriorly so that the tooth has a caniniform appearance. The principal cusp is equal in height to the principal cusp of i^2 and is flanked by two lateral accessory cingulum cusps:

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[1] Further study of this species indicates that it should be transferred to *Myotis* (Hill & Topal, in press).

the lingual cusp is well-developed and prominent but the labial cusp is smaller, less obvious and in the type specimen has been worn away. The anterior upper premolar (pm^2) is large, in the toothrow and separated from pm^4 by a narrow diastema. The lower incisors are tricuspid and stand in the line of the toothrow: as remarked by Thomas, the third is considerably more massive than the other two. The anterior lower premolar (pm_2) is not greatly reduced and is not extruded from the toothrow.

Measurements of B.M. 67.1604, followed by those of the type and paratype specimens: length of forearm 28·8, 28·5, 29·1; greatest length of skull 12·3, 12·7 12·3; condylobasal length 11·6, 11·8, 11·5; condylocanine length 10·9, 11·2, 11·1; width across anteorbital foramina 3·6, 3·5, 3·7; zygomatic width —, 8·0, —; least interorbital width 2·9, 3·0, 3·3; width of braincase 6·2, 6·3, 6·2; mastoid width 6·7, 6·7, 6·8; c^1 c^1 3·4, 3·3, 3·4; m^3–m^3 5·4; 5·3, 5·3; c–m^3 4·4, 4·5, 4·4; length of mandible —, 8·7, 8·7; c–m_3 4·7, 4·8, 4·7.

Pipistrellus societatis sp. nov.

Type and only specimen: ♂ B.M. 67.1605 (in alcohol, skull extracted). Base Camp, Gunong Benom, Pahang, Malaya, 3° 51′ N, 102° 11′ E, 800 ft. Collected 15 March 1967 by Lim Boo Liat and Yong Hoi Sen for the Gunong Benom Expedition, 1967. Original number BM 225.

Diagnosis: Allied to and externally closely resembling *Pipistrellus circumdatus* (Temminck), but differing in smaller size; in greater inflation of the anterior part of the braincase; in its shorter, narrower rostrum which is more inflated laterally; in the absence of well-defined supraorbital ridges; in its more abruptly curved supraorbital margin; in the absence of a deeply excavated frontal depression; narrower narial emargination which is not constricted posteriorly; in having a shorter post-palatal extension with the pterygoid region widened posteriorly; in shallow basial pits which are not sharply excised into the basisphenoid; in shorter toothrows, less massive dentition and much reduced third upper molar, in which the metacone and third commissure have been all but lost.

Description: Externally almost exactly like *P. circumdatus* but with slightly shorter forearm. Dorsal pelage predominantly blackish brown, heavily overlaid by orange or bronze tipping, the individual hairs basally brown, blackish brown for most of their length and profusely but irregularly tipped with orange or bronze. Crown pelage orange tipped but with a small area of straw-coloured, dark brown tipped hairs just anterior to the junction of the aural anterior margin with the head, a feature not so far noted in *circumdatus*. Ventral pelage dark brown, the hairs tipped with greyish white: there is a small wart bearing a few longer, darker hairs medianly situated on the throat just anterior to a line joining the angles of the mouth. Fur extending a little on to the uropatagium but tibia not especially hairy, the digits with a sparse cover of moderate hairs.

Ears large and bluntly rounded, their anterior margin strongly convex in the proximal half, with prominent, posteriorly directed basal lobule. Distal half of anterior margin almost straight, upper part of posterior margin similarly nearly straight but becoming convex with an emargination opposite the base of the tragus and terminating in a wide, quadrangular antitragal lobe, its anterior edge standing squarely to the margin of the ear and to the cheek, inserted a little behind and below the angle of the mouth, forming a small downwardly directed pendent lobule similar to that of *Chalinolobus gouldi*. Tragus large, its sharply concave anterior margin terminating in a rounded, anteriorly directed point: posterior margin strongly convex, its upper part almost horizontal, terminating basally in a large, rounded lobule. Ear margins, especially anteriorly, yellowish white, a feature remarked by Temminck in the original account of *P. circumdatus* and evident to some extent in dried specimens.

Skull short, wide, with rounded, rather globular braincase, inflated and elevated in the frontal region, the lambdoid crests not especially prominent and the sagittal crest lacking. Interorbital region wide, the supraorbital crests only faintly defined, terminating in small tubercles. Frontal depression shallow, with weakly defined boundaries extending anteriorly as a very shallow median sulcus, bordered by wide, low lateral swellings which contrast with the higher, more ridge-like lateral swellings of *circumdatus*. Rostrum short and wide, inflated laterally above anteorbital foramen, the rostrum in frontal aspect having a rounded rather than angular profile as in that species. Supraorbital ridges curving abruptly from the interorbital region to join the anterior margin of the orbit which forms a flange at the side of the rostrum. Narial emargination parallel-sided, almost square posteriorly. Palate short with a narrow anterior emargination a little wider than the distance between the inner faces of i^{2-2}, extending posteriorly to a line joining the back of the canines. Post-palatal extension short, with apparently narrow post-palatal spine, the pterygoid wings divergent posteriorly. Basial pits shallow, not sharply excised into the basisphenoid.

Teeth of type specimen heavily worn: inner upper incisor (i^2) massive, faintly bifid at tip, with small posterior cingulum cusp, outer upper incisor (i^3) approximately one third basal area of i^2 with large central cusp flanked by smaller lateral cusps, its tip reaching slightly above cingulum of i^2, separated from canine by a narrow diastema and pushed forward so that the upper incisors lie almost in a straight line. Anterior upper premolar (pm^2) very small, completely intruded from toothrow: in the type specimen pm^2 is lacking from the right toothrow but a small alveolus can be discerned. Third upper molar (m^3) reduced, narrow, platelet-like: in the type specimen the complete loss of the third commissure is clearly due to wear but it is obvious that this and the metacone are much reduced. Inner (i_1) and second (i_2) lower incisors incipiently four-cusped; i_3 shorter and wider than these, tricuspid. Anterior lower premolar (pm_2) one fourth crown area of pm_4: hypoconid and entoconid of m_3 slightly reduced. Measurements of *P. societatis* and *P. circumdatus* appear in Table 3.

REMARKS: This new species is clearly very closely related to *P. circumdatus*, a poorly known species apparently so far represented only by the female type specimen from Tapos, Java in the Rijksmuseum van Natuurlijke Historie, Leiden (Jentink, 1887 : 277, 1888 : 178); a specimen (B.M. 7.1.1.401) labelled "Java" from the Tomes Collection, now in the British Museum (Natural History) and possibly one of the original specimens; an example (B.M. 61.12.10.1) without skull labelled "India" and also in the British Museum (Natural History); and from a specimen from Pyepat, Upper Burma, recorded by Anthony (1941 : 81) and Tate (1942 : 250) and now part of the collection of the American Museum of Natural History.[1] Through the courtesy of the authorities of the Rijksmuseum van Natuurlijke Historie I have been able to examine the type specimen and I am indebted to Dr. K. F. Koopman who has arranged the loan of the Burmese specimen from the American Museum of Natural History.

Both *P. circumdatus* and *P. societatis* may be readily recognized by their striking coloration, the blackish dorsal pelage having characteristic orange or bronze tips. The skull of *circumdatus*, however, does not seem to have been described except in so far as Tate (1942 : 250) based his group definition on the skull of A.M.N.H. 114850 from Burma. Cranially, *circumdatus* is more massive than *societatis*, its braincase less inflated frontally and with a low sagittal crest. The supraorbital ridges are prominent, terminating in small tubercles, enclosing a deeply excavated frontal depression which extends anteriorly as a shallow rostral sulcus, bound laterally by low longitudinal inflations which converge to merge anteriorly. Rostrum longer and broader than in *societatis*, the area above the anteorbital foramen uninflated but instead sloping more abruptly from the inflations bordering the rostral sulcus to give the rostrum in frontal aspect an angular rather than rounded outline. Supraorbital ridges curving less abruptly from the interorbital region than in *societatis*, the anterior margin of the orbit forming a flange as in that species. Narial emargination narrowed posteriorly with a rounded apex, the anterior palatal emargination equal in width to the distance between the inner faces of i^{2} ^{2} or slightly exceeding it and extending posteriorly almost to a line joining the posterior faces of the canines. Post-palatal extension slightly longer than in *societatis*, with narrow post-palatal spine, the pterygoid wings parallel: basial pits prominent, deep, sharply excised into the basisphenoid. Dentition as described for *P. societatis* but teeth larger and more massive, m^3 not reduced but with well-developed metacone and clearly evident third commissure, while m^3 has the hyopconid and entoconid unreduced. The skull of the Burmese example differs from the skulls of the type and second Javan specimens in slightly smaller size, less prominent cranial crests, its supraorbital ridges terminating in slight tubercles which are barely evident in the Javan examples, in a shallower frontal depression, shorter post-palatal extension and narrower post-palatal spine, and slightly less massive dentition. It is possible therefore that adequate series of specimens may show the mainland and Javan populations to be subspecifically distinct.[1]

The name of the new species is selected in allusion to the combined effort of the several members of differing nationalities and institutions who constituted the Gunong Benom Expedition, 1967.

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[1] Lord Medway has now obtained (1971) a specimen of *P. circumdatus* from Fraser's Hill, Pahang. It agrees closely with the Burmese example.

TABLE 3

MEASUREMENTS OF *Pipistrellus societatis* AND *P. circumdatus*

	Pipistrellus societatis B.M. 67.1605 Type Malaya	*Pipistrellus circumdatus* Leiden "a" Type Java	*Pipistrellus circumdatus* B.M. 7.1.1.401 Java	*Pipistrellus circumdatus* A.M.N.H. 114850 Burma
Length of forearm	37·6	42*	43·6	41·6
Greatest length of skull	15·3	—	—	15·5
Condylobasal length	14·4	—	15·7	14·9
Condylocanine length	14·1	—	15·4	14·7
Palatal length (excluding post-palatal spine)	6·6	—	8·4	7·6
Length palatal bridge (excluding post-palatal spine)	5·0	—	6·6	6·1
Length orbit – gnathion	3·6	4·2	4·2	4·3
Width across anteorbital foramina	5·1	5·5	5·6	5·3
Lachrimal width	6·7	7·2	7·4	7·3
Width across supraorbital tubercles	6·0	6·7	6·6	6·7
Zygomatic width	10·4	—	—	10·8
Least interorbital width	4·3	4·2	4·4	4·4
Width of braincase	7·9	—	—	7·9
Mastoid width	8·5	—	—	8·5
c^1–c^1	4·6	5·2	5·2	4·9**
m^3–m^3	6·7	—	7·5	7·1
c–m^3	5·2	6·2	6·4	6·0
Length of mandible	10·4	—	12·1	—
c–m_3	5·6	6·5	6·7	6·4

* From Tate (1949 : 292)
** Right upper canine damaged

Hesperoptenus blanfordi (Dobson, 1877)

♀ B.M. 65.345 (in alcohol, skull extracted). Jenka, Temerloh, Pahang, 3° 37′ N, 102° 30′ E. Collected and presented by the Earl of Cranbrook.

Described originally from Tenasserim, this species is relatively rare in collections but is recorded by Anderson (1881 : 133) from Johore and by Robinson and Kloss (1915 : 116) from Khao Nawng, Bandon, Lower Thailand, while Thomas (1916 : 2) lists specimens from the Semangkko Pass, below Fraser's Hill, on the Selangor-Pahang boundary; Gunong Tampin, Negri Sembilan; Telok Bahang (= Rahang), Penang, and from Kuala Lumpur, Selangor. The specimen listed from Khao Nawng by this author is doubtless that previously recorded by Robinson and Kloss. The species is easily recognized by its small size (length of forearm 26–28), the presence of a broad, well-developed pad at the base of the thumb extending to the base of the second metacarpal, and by the small size and extreme displacement of the outer upper incisor (i^3) which is intruded from the toothrow to the extent that it lies directly behind the large inner upper incisor (i^2), in contact with the posterior face of that tooth and with the lingual face of the canine.

Davis (1962 : 42) recorded a specimen from the Sapagaya Forest Reserve, Sandakan, Sabah (5° 37′ N, 118° 04′ E) as *Hesperoptenus doriae*. Through the kindness of Dr. J. C. Moore of the Field Museum of Natural History, Chicago, I have been able to borrow and examine this specimen, F.M. 77025. As Davis points out, it is a juvenile male. However, it is much larger than the adult type specimen of *Hesperoptenus doriae* and agrees very closely with the type specimen of *H. tomesi*, described by Thomas (1905 : 575) from Malacca, to which it must be referred. *Hesperoptenus tomesi* has been known hitherto only from the type specimen and the example from Sabah is therefore the first record for Borneo. It may be recognized by its large size (length of forearm c. 50) which is similar to that of the Indian *H. tickelli*, by its rich, dark brown colour, by its displaced outer upper incisor and by its strongly imbricated lower incisors. *Hesperoptenus doriae* is smaller (length of forearm 38·0) and is (from specimen in spirit) pale brown, with the outer upper incisor not displaced from the toothrow and the lower incisors not much imbricated.

Murina huttoni (Peters, 1872)

♂ B.M. 67.1606 (in alcohol, skull extracted). Near Camp 4, Gunong Benom, Pahang, 3° 51′ N, 102° 11′ E, 4800 ft. 17 March 1967.

This species establishes the presence of *M. huttoni* in Malaya, whence *M. suilla*, *M. cyclotis* and the striking *M. aenea* have already been recorded (Hill, 1964). Although very similar to *M. cyclotis peninsularis* in external appearance, this species may be readily distinguished by the features of its molar teeth, the mesostyles of m^{1-2} being more developed than in *M.c. peninsularis* with the paracones and protocones less reduced, and especially by the unreduced hypoconids and entoconids of m_{1-2}, which are separated from the protoconids and metaconids by a wide trough. These features indubitably refer the specimen to *huttoni:* in *cyclotis* the mesostyles, paracones and protocones of m^{1-2} are reduced and in m_{1-2} the hypoconids and entoconids are much reduced, sometimes barely evident, and are only narrowly separated from the protoconids and metaconids. The degree of reduction is less apparent in m_3. Subspecific determination of the specimen is less certain: in dorsal coloration it resembles *M.h. rubella* from Fukien, the hairs with bright golden brown subterminal annulations as in that subspecies.

MEASUREMENTS: length of forearm 34·1; greatest length of skull 17·5; condylobasal length 15·6; palatal length 8·5; length orbit-gnathion 4·5; rostral width 5·5; zygomatic width 9·4; least interorbital width 4·3; width of braincase 7·5; height of braincase 6·1; mastoid width 8·0; c^1–c^1 4·3; m^3–m^3 5·5, c–m^3 5·8.

Murina cyclotis peninsularis Hill, 1964

♀ B.M. 67.1607 (skin and skull). Base Camp, Gunong Benom, Pahang, 3° 51′ N, 102° 11′ E, 700 ft. 20 February 1967.

♂ B.M. 68.845 (in alcohol, skull extracted). Waterworks Road, Batu Pahat, Kangar, Perlis, c. 6° 27′ N, 100° 12′ E. 4 January 1968.

These specimens are the first examples of this subspecies to be recorded since its description (Hill, 1964). Although in some dimensions the specimen from Perlis is similar to *M.c. cyclotis*, it agrees with *M.c. peninsularis* in having the rostrum wide anteriorly, with toothrows which are not especially convergent, and in massive canines, premolars and molars. Measurements (B.M. 67.1607, B.M. 68.845): length of forearm 38·8, 34·7; greatest length of skull 18·6, 17·4; condylobasal length 16·7, 15·4; length orbit-gnathion 4·5, 4·3; palatal length 9·2, 8·2; rostral width 6·0, 5·8; zygomatic width 10·9, 9·9; least interorbital width 4·5, 4·3; width of braincase 8·1; 8·0; height of braincase 6·7, 6·7; mastoid width 9·1, 8·5; c^1–c^1 5·1, 4·5 m^3–m^3 6·0, 5·6; c–m^3 6·2, 5·5.

Shamel (1942 : 327) recorded two specimens from northern Thailand as *M. toxopei*, described by Thomas (1923 : 254) from the island of Buru in the Moluccas. From the description and measurements given by Shamel it seems more probable that these specimens represent *M. cyclotis*.

Miniopterus schreibersii blepotis (Temminck, 1840)

♂♂ B.M. 67.216-217 (skins and skulls). Pine Tree Hill, Fraser's Hill, Pahang, 3° 43′ N, 101° 42′ E, 4250 ft. 12 October 1966.

♂ B.M. 67.218 (in alcohol). Fraser's Hill, 4750 ft. 22 October 1966.

Although known to occur from mainland localities as far south as Koh Lak in southern Thailand (specimen in British Museum (Natural History)) and from Sumatra, Java and Borneo, there seems to be no published record of *M. schreibersii* from Malaya, whence these specimens now establish it. Measurements of B.M. 67.216–217: length of forearm 44·8, 50·8; condylobasal length 15·0, 16·3; condylocanine length 14·1, 15·5; zygomatic width 9·0, 9·4; least interorbital width 4·0, 4·2; width of braincase 8·1, 8·5; m^3–m^3 6·6, 7·4; c–m^3 6·0, 6·5. The length of forearm in B.M. 67.218 is 49·3. The large example (B.M. 67.217) agrees almost exactly with a similarly large specimen from Kok Lak, further north on the east coast of Lower Thailand.

Small specimens of *M. schreibersii* are difficult to distinguish from large examples of the sympatric species *M. medius*. However, apart from its usually longer forearm, *M. schreibersii* differs from *medius* in longer skull and wider palate: specimens from Java, Malaya and Indochina have a length of forearm of 43·6–50·8, condylobasal length 14·7–16·3, condylocanine length 13·8–15·5 and m^3–m^3 6·5–7·4 while specimens of *medius* from Java and Pulau Kaban (off the east coast of Johore, States of Malaya) have a length of forearm of 40·8–43·1, condylobasal length 13·8–14·3, condylocanine length 13·1–13·5 and m^3–m^3 5·8–6·3.

Miniopterus medius Thomas and Wroughton, 1909

♀ B.M. 67.1610 (skin and skull). Bukit Cheras, Panching, near Kuantan, Pahang, 3° 53′ N, 103° 09′ E. 17 February 1967.

This is a further Malayan record for the species, hitherto known on the mainland only from Gunong Pondok, Perak (Chasen, 1926 : 156) but also recorded from Pulau Kaban, off the east coast of Johore, and from Pulau Terutau, southern Thailand by Thomas (1916 : 4). Measurements: length of forearm 42·2; greatest length of skull 14·4; condylobasal length 13·8; condylocanine length 13·0; zygomatic width —; least interorbital width 3·7; width of braincase 7·7; mastoid width 8·1; c^1–c^1 4·0; m^3–m^3 5·9; c–m^3 5·4. Measurements of other specimens from eastern Pahang (supplied by Lord Medway) (♂♂♀ Medway 66.46–48) length of forearm (Medway 66.47–48 only) 43; condylobasal length 13·8–14·0; condylocanine length 12·9–13·2; m^3–m^3 5·8–5·9.

SUMMARY

Taxonomic notes on the more unusual species of bats obtained by the 1967 Expedition to Gunong Benom are presented in this paper, with similar accounts of other specimens of taxonomic interest obtained in recent years in Malaya by Lord Medway and his associates. The genus *Coelops* is reviewed so far as available material permits, with the recognition of two valid species, *C. frithii* and *C. robinsoni*. A new species, *Pipistrellus societatis*, is described from Gunong Benom: *Rhinolophus malayanus*, *R. robinsoni* (?) *klossi*, *R. macrotis dohrni*, *Coelops frithii*, *Myotis siligorensis* and *Murina huttoni* are added to the bat fauna of the States of Malaya while additional specimens of *Hipposideros lylei*, *Myotis horsfieldii horsfieldii*, *Myotis hasseltii*, *Pipistrellus ridleyi*, *Hesperoptenus blanfordi*, *Murina cyclotis peninsularis*, *Miniopterus schreibersii blepotis* and *M. medius* are recorded. *Hesperoptenus tomesi* is recorded for the first time from Borneo from a specimen hitherto thought to be *H. doriae* and an example of anomalous dentition in *Pipistrellus javanicus* is described.

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THE GUNONG BENOM EXPEDITION
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A. G. C. GRANDISON

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By ALICE G. C. GRANDISON

INTRODUCTION

Gunong Benom offered the herpetologist wide scope for sampling the reptiles and amphibians of both virgin and disturbed rain forest formations and for studying the altitudinal zonation of the species in natural climax vegetation. In the time available on the 1967 expedition it was possible to carry out only a relatively superficial survey, nevertheless the material collected included not only 79 known species of reptiles and amphibians, of which a few constituted additions to the West Malaysian fauna, but also an undescribed species of snake.

Base Camp was ideally situated in an area containing a wide variety of terrestrial, arboreal and riparian habitats in primary rain forest as well as in both recent and well established secondary growth in areas of disturbance associated with logging (see Whitmore, no. 2 of this volume). The many aquatic situations differed greatly in extent and flow. However, as expected, the specimens of greatest scientific interest were found at higher elevations, from 3–6000 ft, and it is unfortunate that more time and personnel could not have been employed in obtaining longer series of the forms from these altitudes. It is possible that streams at elevations beyond 4000 ft, harboured species in addition to those obtained near the two highest camps, for the partially underground stream near camp 4 at 5000 ft, being somewhat inaccessible and reached only by a precipitous, unstable and hazardous route, was not thoroughly searched after dark, nor was the broad, fairly shallow and fast flowing stream that appeared for a short distance above ground at ca 5800 ft. While no frog other than *Metaphrynella pollicaris* was heard above 5100 ft it is likely that the West Malaysian species known to occur at high elevations in other parts of their range have similar vertical distributions on Gunong Benom.

The herpetology of some of West Malaysia's neighbours, notably of Borneo, the Philippines and Thailand, has fairly recently been reviewed and excellent detailed monographs on the taxonomy and zoogeography have been published (Inger 1954 & 1966, Taylor 1962, 1963 & 1965). In contrast, the only major works on the herpetofauna of the Malayan peninsula were either published decades ago (Boulenger 1912, Smith 1930) or deal only with snakes (Tweedie 1954). Boulenger's 1912 work and Smith's 1930 list which is a supplement to Boulenger's, are still extremely useful reference books, despite their outdated nomenclature and subsequent additions to the list of species known in the peninsula. Tweedie's (1954) and Lim's recent reports have made significant contributions towards an understanding of the habits and distribution of snakes in the peninsula, but only Boulenger (1908), Smith (1922) and Lim (1963, 1964 & 1967) have reported collections from above 5000 ft.

ALTITUDINAL ZONATION

Boulenger (1908) reporting on the herpetological collection made by Wray and Robinson on Gunong Tahan mentions only four species taken at above 5000 ft: *Leptobrachium gracile* (5200 ft), *Rana hascheana* (5200 ft), *Rana Larutensis* [*Amolops larutensis*] (5200 ft) and *Psammodynastes pulverulentus* (5–5800 ft). Smith (1922) recorded the following additional species found on Gunong Tahan at similar altitudes:

Polydontophis collaris [Sibynophis collaris]	5400–5700 ft
Calamaria pavimentata	5400–5700 ft
Goniocephalus robinsoni	5400–5700 ft
Calotes floweri	6400 ft
Lygosoma [Siaphos] larutensis	5400–5700 ft
Philautus vermiculatus	5000 ft

From similar elevations on Gunong Benom only three of these Tahan species were obtained (*Amolops larutensis, Leptobrachium gracile* and *Philautus vermiculatus*) but five additional species were found, namely:

Pareas vertebralis	5000 ft
Macrocalamus sp. nov.	5800–6500 ft
Microhyla annectans	5000 ft
Metaphrynella pollicaris	5500–6250 ft (also 2950–4300 ft)
Philautus aurifasciatus	5000 ft

To these can be added the following high altitude snake species reported on by Lim (1963, 1964 & 1967) and collected on Gunong Brinchang in the Cameron Highlands, Pahang:

Typhlops diardi muelleri	5500 ft
Cylindrophis rufus	5500 ft
Elaphe porphyracea	6300 ft
Calamaria fraseri [C. lowi gimletti]	5000 ft
Calamaria gimletti [C. lowi gimletti]	5000 ft
Calamaria lumbricoidea	5500 ft
Collorhabdion williamsoni	6000 ft
Macrocalamus lateralis	5200–6300 ft
Macrocalamus tweediei	5000–6000 ft
Ahaetulla ahaetulla	5000 ft
Ahaetulla caudolineata	5000 ft
Chrysopelea paradisi	5000 ft
Lycodon butleri	6664 ft
Natrix chrysarga [Rhabdophis chrysarga]	5500 ft
Natrix sanguinea [Amphiesma sanguinea]	5500 ft
Natrix sarawakensis [Amphiesma sarawacensis]	5400–5500 ft
Pseudoxenodon macrops	6000 ft
Boiga jaspidea	5000 ft
Trimeresurus popeorum	5500 ft
Trimeresurus monticola	5700 ft
Gymnodactylus pulchellus [Cyrtodactylus pulchellus]	5000–6000 ft

Lim also provided useful information on the habitat preferences of the 18 species that he collected, as well as analyses of stomach contents.

In retrospect, it is obvious that on Gunong Benom it would have been worthwhile engaging the services of nimble tree climbers to search the canopy and the high side branches of well established secondary growth flanking the track. Such exercises would almost certainly have yielded longer series of *Philautus vermiculatus*, possibly female *Metaphrynella pollicaris*, some of the high altitude forms reported by Smith (1922) and by Lim (1963, 1964, 1967) and maybe other species. Many pairs of hands would have to be employed and a great deal of work done both by night and by day before it could be claimed that adequate sampling of Gunong Benom's herpetofauna had been accomplished. The results of the 1967 survey certainly suggest that the area would repay further and more intensive study.

Detailed taxonomic accounts for most of the species obtained on G. Benom have been omitted from this report since a high proportion of them occur also in either Thailand or Borneo, or both, and full descriptions of each species are available in Taylor's (1962, 1963, 1965) and Inger's (1966) monographs.

METHODS AND TERMINOLOGY

Measurements taken with dial calipers reading to 0·1 mm were as follows:

Body length: combined length of head and body, that is equivalent to the distance from snout to vent (abbreviated in text S–V).

Head length: the distance from the tip of the snout to the jaw articulation.

Head width: the greatest width of the head, usually at the position of the tympana.

Length of tibia: the distance from the convex surface of the knee to the convex surface of the tibio-tarsal joint, the measurement taken with the leg flexed.

Length of first toe: the distance from the tip of the digit to the proximal edge of the basal subarticular tubercle.

Length of fourth toe: the distance from the tip of the digit to the proximal edge of the basal subarticular tubercle.

Other measurements are explained where they appear in the text.

Ranges given for each species are based on published records and on material in the British Museum collections but records from the literature are quoted only if from the species accounts I can be reasonably confident that the identifications are correct. 'Borneo' is used here to refer to the whole island and thus embraces E. Malaysia (Sabah and Sarawak), Brunei and Kalimantan. 'W. Malaysia' is employed in preference to 'The States of Malaya' and is defined as the peninsular portion of the Federation of Malaysia; it thus excludes the provinces of Thailand south of the Isthmus of Kra.

Unless otherwise stated, all specimen numbers are those of the British Museum (Natural History).

GYMNOPHIONA

Family **ICHTHYOPHIIDAE**

Caudacaecilia nigroflava (Taylor)

Ichthyophis nigroflavus Taylor 1960 : 101.

MATERIAL: BM 1967.2775–80 (1 adult, 5 metamorphosed juveniles).

HABITAT: The juveniles were found in mud and in sand at the margin of the stream near Base camp, 700 ft, during late afternoon. The adult (total length 420 mm) was found swimming in a 2 ft deep part of the clear, fast-flowing stream at Base camp.

COLOUR IN LIFE: The adult was a bluish-black with a clearly defined yellow, lateral stripe extending from below the eye to the vent. The stripe is also visible in the juveniles but in life was more cream and the body rather brownish.

REMARKS: I am indebted to Professor E. H. Taylor for the identification of these specimens.

RANGE: W. Malaysia, Sumatra and Borneo.

SALIENTIA

Family **BUFONIDAE**

Ansonia leptopus (Günther)

Bufo leptopus Günther 1872 : 598.

Material: BM 1967.2765–70 (1 ♀, 5 ♂).

Habitat: The specimens were obtained in a 200 yd stretch of the fast-flowing tributary of the River Kerau about 500 yds downstream from Base camp, 700 ft, at a point where the stream is bordered by dense primary forest. Four of the males were caught on top of stones in midstream while the fifth male was taken in amplexus with the female under a stone at the edge of the stream where the water formed shallow, still pools among stones and gravel.

Colour in life: Dorsum uniform brown. Venter spotted yellow or orange.

Call: A soft chirp.

Remarks. These specimens belong to the group of *Ansonia* species in which the tympanum is visible and the first finger reaches to the disk of the second. The only species in this group that is known to occur in the Malayan peninsula is *A. penangensis* but conspecificity with *penangensis* can be ruled out on account of size differences (topotypical *penangensis* gravid female measures 37·5 mm S–V while the gravid G. Benom female measures 51·0 mm) as well as differences in colour pattern, webbing and in the complete absence of a tarsal ridge in the G. Benom material. Bornean *A. leptopus* and *A. longidigita* also belong to this group and the G. Benom specimens have been compared with the holotypes and other examples of these species. The holotype of *leptopus* which is a gravid female is now flabby and somewhat faded but in size, snout shape, webbing and in the remnants of its ventral pattern there is close similarity to the Benom female. Its dorsum however is more coarsely granulate than in the Benom specimen but as Inger (1960) has pointed out, there is considerable variation in tuberculation in this species. The males have vocal sacs and openings, and nuptial pads developed over the entire dorsal surfaces of the first fingers; they vary in body length from 36·0–39·3 mm (average 37·7 mm). They are slightly more warty than the female and the short, oblique series of rather prominent warts above the tympanum in the holotype and in the Benom female is rather less well developed. In both sexes there is a single row, but occasionally double row of dark tipped spinules along both the upper and lower lips, along the canthal and supraorbital edges and as a vertical row at the tip of the snout.

Range: W. Malaysia and Borneo.

Ansonia ?tiomanica Hendrickson

Ansonia tiomanica Hendrickson 1966 : 74.

Material: BM 1967.2771–73 (2 ♀, 1 ♂).

HABITAT: All three individuals were found at night on leaves in the boulder strewn stream bed in the valley at ca 3400 ft below camp 3.

REMARKS: These specimens belong to the group of *Ansonia* species that have a visible tympanum and are without a tarsal ridge and in which the tip of the first finger does not reach as far as the disk of the second finger when the digits are adpressed. This group comprises the West Malaysian species *malayana* Inger and *tiomanica* Hendrickson, the Bornean and Sarawakian species *fuliginea* (Mocquard), *hanitschi* Inger, *platysoma* Inger, *latidisca* Inger and the S.W. Indian *ornata* Günther (Inger 1960).

The G. Benom material has been compared with type and other material of those species, except *tiomanica* of which no specimens at all were available, and while they have more characters in common with *malayana* and *tiomanica* than with the other species, there are distinctive differences.

DESCRIPTION: Habitus moderately slender; head slightly wider than long (measured from lower tip of snout to posterior rim of tympanum); snout truncate but a little pointed at tip, sloping in profile, nostril above or slightly anterior to symphysis; canthus rostralis sharp and slightly curved, lores straight and vertical; tip of snout laterally compressed, forming a well developed median, vertical ridge; interorbital

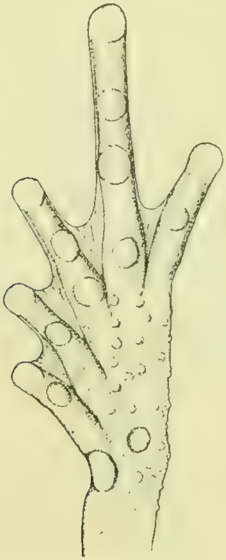


FIG. 1. Ventral view of the foot of *Ansonia ?tiomanica* (B.M. 1967.2773).

at narrowest point wider than upper eyelid; tympanum distinct, its horizontal diameter about half eye diameter and half internarial distance. Fingers slender, tips rounded, not wider than rest of fingers, no rudimentary web; first finger much shorter than second, length of first (measured from median edge of outer palmar tubercle) equal to eye diameter; fourth finger longer than second; subarticular tubercles feeble; a low, round, outer palmar tubercle. Tips of toes swollen into small, round disks; fifth toe longer than third by length of disk; broad webbing on toes leaves the following phalanges free from web in both sexes:

1st	2nd	3rd	4th	5th
½	½	2–2½ : 1½–2	3–3½ : 3–3½	2

Subarticular tubercles weak; two metatarsal tubercles, the outer oval, low and barely discernible, the inner round, slightly conical and much more conspicuous; no tarsal ridge.

Skin above markedly tuberculate with round, well spaced warts, the largest and most conspicuous above and below the tympanum, in a line along the dorsolateral edge and on the flanks, each wart surmounted by usually one small, white or horn-tipped, conical tubercle. On top of head, on back and on upper surfaces of limbs similar but smaller warts of varying size all with spinose tips, those warts on limbs particularly spinose; interspaces shagreened. Surfaces of abdomen coarsely granular with scattered, small, spinose tubercles. Similar spinose tubercles scattered under chin and throat of females; in males spinose tubercles are horn-tipped and confined to 3–4 rows under mandible. A longitudinal opening into subgular vocal sac developed on right side of mouth but no nuptial asperities. Colour in life dark brown with yellow chrome spots on both upper and lower surfaces. A very prominent yellow chrome wart at angle of jaws below posterior rim of tympanum, its diameter at least 2/3 the tympanic diameter, much larger and more elevated than the yellow tubercles in the same area on two of the Perak paratypes of *malayana*. Upper and lower lips spotted yellow chrome. In two of the specimens a dark brown cruciform pattern on the back can be detected. This pattern is reminiscent of the *malayana* pattern which is particularly well developed in the Thailand paratypes and consists of two clearly marked crosses, one between the shoulders, the other immediately behind, and between the two 'Xs' a light patch but in neither G. Benom specimen is the interscapular light spot evident and the arms of the crosses are obscure. Limbs with indistinct light bars on which there are numerous yellow spots. Undersurfaces of head, body and limbs dusky with numerous very small yellow chrome spots similar to the Perak holotype and paratypes of *malayana*.

A. malayana is known to occur in the Larut Hills, Perak at 3–4000 ft and at Chumporn, Tasan, S. Thailand. British Museum individuals obtained at Ipoh and on G. Tahan may also be referable to this species. From *malayana* the G. Benom specimens differ in the following characters:

1. Absence of sexual dimorphism in the extent of toe web.
2. Several rows (3–4) of very small, closely set spinules under the mandible (in *malayana* males a single row of well-spaced spinose tubercles).

3. Greater body length. In G. Benom specimens the female measures 30·2 mm from snout to vent and the male 25·4 mm, whereas the female paratypes of *malayana* vary from 26·0–28·0 mm and the four mature males 20·2–23·2 mm.
4. A large, conspicuous yellow wart at the angle of the jaws whose diameter is at least 2/3 the tympanic diameter.
5. A more tuberculate dorsum.
6. Slightly less webbing on the 3rd and 5th toes.

A. tiomanica is known from only the two syntypes, an adult female and an adult male taken at Ulu Lalang, Pulau Tioman. Comparison with this species is hampered not only by an absence of material but by the discrepancies between Hendrickson's description of the types and the figures he gives of the hand and foot (1966). He describes the disks of *tiomanica* as being spatulate but the drawings show rounded tips similar to those of *malayana* and of the G. Benom individuals. The tips of the 3rd and 4th fingers although described as being twice as wide as the narrowest portion of those digits are not so figured and the number of phalanges free from web is considerably greater in the figure than in the text. If one assumes that Hendrickson's text is accurate there is apparently little to distinguish the G. Benom specimens from *tiomanica*, except greater size (*tiomanica* ♀ 36·3 mm, ♂ 31·2 mm), absence of mandibular asperities, the greater elevation of the inner metatarsal tubercle, the presence of a central, low metatarsal tubercle and possibly also a more reduced web on the 1st and 2nd toes although no details are given of the extent of the web on those digits. The difference in mandibular asperities might well be a reflection of the sexual maturity of the male *tiomanica* and the other differences due to geographical variation and until longer series are available assignment of the G. Benom specimens to *tiomanica* can be only tentative.

Bufo asper Gravenhorst

Bufo asper Gravenhorst 1829 : 58.

MATERIAL: BM 1967.2726–37, 2774 (1 ♀, 7 ♂, 2 halfgrown, 2 juveniles, 1 skeleton).

HABITAT: All adults were obtained from the boulder strewn tributary of the River Kerau or from its immediate vicinity at ca 700 ft. At night numerous individuals were to be seen between and on the large boulders, particularly at the side of a quiet deep backwater close to Base camp. On the forest litter near the stream at camp 3 and on the laterite logging track near camp 1 other examples were taken. No *Bufo asper* were seen or heard on G. Benom above 3430 ft.

RANGE: Peninsular Thailand and Burma, to Java and Borneo (Inger 1966).

Bufo parvus Boulenger

Bufo parvus Boulenger 1887 : 346.

MATERIAL: BM 1967.2738–58 (1 ♀, 19 ♂, 1 juvenile).

HABITAT: The series was obtained mainly from the floor of disturbed forest at 700 ft, most individuals being under twigs and felled branches in muddy patches, within 200 yds of the stream. One male was taken on bare clay some 500 yds from water. A pair in emplexus were at the margin of the stream where the water was shallow and with little current. One specimen was found in virgin forest at 1600 ft.

COLOUR IN LIFE: The paratoids, limbs and the vertebral blotches pinkish, the general ground colour of the dorsum russet brown. The throat, belly and undersurfaces of hind limbs light grey or cream, lightly spotted with dark brown. The throat of one male blackish.

CALL: crow-ack repeated quickly six times and followed by a short interval.

RANGE: Peninsular parts of Burma, Thailand and Malaya, Sumatra (Taylor 1962).

Cacophryne borbonica (Tschudi)

Hylaplesia borbonica Tschudi 1838 : 70.

MATERIAL: BM 1967.2759–60 (1 ♂, 1 ♀).

ECOLOGY: Found at ca 700 ft on Benom, a considerably lower elevation than has previously been reported for the species. Inger (1966) reported that *borbonica* has been taken from 600–1500 metres in Borneo and Sumatra, and in Thailand specimens have been found in hilly country. The adult female was found after heavy rain, in disturbed forest at night on the dead branch of a low bush at approximately 18″ from the forest floor, at the edge of the Base camp track. The male was taken on the steep clay bank of a still backwater of the stream close to Base camp.

COLOUR IN LIFE: Ground colour of upper surfaces of the female greyish-brown with a pair of black mid-dorsal spots between the orbits and between the paratoid glands. On the middle of the back in the sacral region there is a conspicuous hourglass-shaped dark mark, which is separated from the occipital spots by a light diamond-shaped area. The dorso lateral series of glandular tubercles is noticeably lighter than adjacent areas. Upper lips spotted dark brown. Irregularly-shaped dark blotches on flanks that have a tendency to form oblique stripes. Limbs with dark crossbars. Groin, inside of knee and heel joint pinkish-red. Belly cream; throat and chest brownish. The only pattern visible in the male consists of a pair of small dark inter-orbital spots, a pair of dark sacral spots and somewhat indistinct labial spots and cross bars of the limbs. Throat and chest although brownish are lighter than in the female.

SECONDARY SEX CHARACTERS: Sexual dimorphism is marked, the female, which has enlarged darkly pigmented ova, being 42·5 mm while the male, which has a median subgular vocal sac with a long slitlike opening on the left side of the floor of the mouth and nuptial asperities on the entire dorsal aspect of the first finger and median surface of the first metacarpal, measures 27·7 mm. Comparable size difference between sexes was noted by Inger (1966) for equally mature Bornean samples.

RANGE: Peninsular Thailand and Malaya, Sumatra, Java and Borneo (Inger 1966).

Pelophryne brevipes (Peters)

Hylaplesia brevipes Peters 1867 : 34.

MATERIAL: BM 1967.2761–4 (1 ♂, 1 ♀, 2 hgr. ♀).

HABITAT: Number 2761 was found by torchlight at night and 2762 in daylight during the morning after heavy rains, 2 ft from the forest floor on a sodden tree stump near the edge of a stream in the valley below camp 2, about 1600 ft. Examples 1967, 2763–4 were taken near Base camp, on the rough bark of a tree, about 5 ft from the ground, by the side of a disused logging track at approximately 800 ft.

COLOUR IN LIFE: The most striking feature of the colour pattern, particularly at night in torchlight, was the creamy yellow band of varying width which starts below the eye, passes below the tympanum and extends backwards to the groin, leaving a dark brown spot on the upper lip in front of the jaw angle and merging on the flanks with the yellowish, black spotted venter. The band was bordered above by a narrow dark chocolate brown zone. The upper surface of the head and the median dorsal area that is of cruciform shape, a yellow-brown with orange-red tubercles. The cruciform area was outlined in chocolate brown, the sides of the body reddish brown with numerous orange-red tubercles. The throat of the adult male was grey-brown mottled with yellow, that of the female predominantly yellowish with dark brown spotting. The limbs were yellow-brown with dark brown crossbands and orange-red tubercles. The iris was orange-red.

REMARKS: These specimens closely resemble the syntypes of *Nectophryne signata* Blgr. and cruciform patterned examples of *Pelophryne brevipes* as described by Inger (1966) who placed *signata* in the synonymy of *brevipes*.

SIZE: The female with enlarged ova measures 18·8 mm in body length, the two immature females 17·2 and 17·5 mm. The male which has a vocal sac, single rows of mandibular spines and poorly developed thumb pads measures 16·3 mm from snout to vent.

RANGE: Malay peninsula including Aor Island and Singapore, Natuna Islands, Mentawei Islands, Sumatra, Borneo and Mindanao (Inger 1966).

Family **MICROHYLIDAE**

Chaperina fusca Mocquard

Chaperina fusca Mocquard 1892 : 35.

MATERIAL: BM 1967.2665–69 (2 ♂, 4 ♀).

HABITAT: 1650–1750 ft near camp 2. One example was caught under a fern on wet clay at the side of the track, and one specimen was obtained on wet clay close to a sodden fallen log above the section of the small stream in which *Leptobrachium heteropus* occurred on the low plants. Other examples, taken nearer to camp, were found in amplexus at night in small 2″ deep pools in the track formed by prolonged rain in footprints. Although the water in these pools was turbid, no doubt due to the intensity of the rain stirring up the soil, it was humus free. Inger (1966), on the other hand, found that mating *fusca* were always in pools rich in humus and never in ones that lacked putrid material.

COLOUR IN LIFE: Upper surfaces of body jet black with numerous tiny whitish-yellow flecks. Limbs brown with darker brown crossbars and scattered light flecks. Belly with a bold reticulate pattern of citron yellow and black.

RANGE: The occurrence of this species in Pahang extends its known range. The only West Malaysian State from which Inger (1966) recorded the species is Perak. Elsewhere *C. fusca* occurs in Borneo and the southern Philippine Islands.

Kalophrynus pleurostigma pleurostigma Tschudi

Kalophrynus pleurostigma Tschudi 1838 : 86.

MATERIAL: BM 1967.2670 (1 ♂).

HABITAT: At 700 ft in disturbed primary rainforest. Under dead leaf in a ditch at side of logging track close to Base camp. Calling at night.

RANGE: W. Malaysia, Sumatra, Borneo, S. Philippines (Inger 1966).

Metaphrynella pollicaris (Boulenger)

Phrynella pollicaris Boulenger 1890 : 37.

MATERIAL: BM 1967.2695–2719 (1 ♀, 23 ♂, 1 juvenile).

ECOLOGY: Between 2950 and 6250 ft. Except for BM 1967. 2719, the entire series consists of adult males and one gravid female obtained from holes in trees between 4 and 30 ft from the forest floor. No tree that was less than 3″ in diameter was found to harbour the species. The elliptical holes, possibly made by the larvae of long horn beetles, continued down the centre of the tree trunks and at their bases, sometimes a foot below the opening to the exterior, in a pool of peaty water a specimen or a pair were to be found. At the time of the G. Benom visit I was unfamiliar with Wray's method (1890) of expelling *pollicaris* from their tree holes by first pouring in water then dropping in salt. His technique was apparently not only fruitful but would be less damaging to the frogs and to their niches than our practice of opening up the holes with a bush knife. The highest elevation at which *pollicaris* was present on Benom seems to be 6700 ft at which height it was still to be heard. Above 3500 ft it was the only anuran heard calling both by day and by night. It was not heard on the true summit nor on subsidiary summits where the vegetation was drier (leptospermum, orchids and rhododendrons) and the trees on average much shorter (15–20 ft), but only on the slopes, in the valleys and at certain elevations on the ridge followed by the expedition. On the narrow ridge between 4300 and 5500 ft no examples were obtained and no calls of *pollicaris* were heard so there seems to be a gap in the vertical distribution of this species on Benom.

Wray, who obtained the type specimen in the Larut Hills, described the call as 'a loud flute-like musical note uttered at irregular intervals principally during the night' (in Flower 1896) and as 'pretty flute-like notes' (Wray 1890). On Benom the call of *pollicaris* emitted by a single individual was usually a single 'COOP' repeated at regular 15 sec. intervals but in areas where several individuals were calling the sound resembled distant cow bells. The pitch and volume of the call seemed to be related to the size and depth of the cavity occupied by the frog, a loud deep burp being emitted from individuals occupying large deep holes and a lighter thinner 'COOP' from those in narrow holes with slit-like openings. A similar observation on the resonant qualities of the hole was made by Wray (in Flower 1896).

Despite thorough searching, the litter and low vegetation yielded no adult *pollicaris*. One juvenile, BM 1967. 2719, was found on a fern about a foot above the forest floor at 3500 ft close to camp 3 soon after the botanist's collectors had been active in the tree canopy. It seems possible that *M. pollicaris* normally occupies the canopy and that adults descend to tree-holes solely for breeding purposes. This mode of life would explain the absence of the species from low trees, bushes and the forest floor. (The juvenile discovered close to the ground could have been dislodged by the botanical collectors working in the high branches.) It would further account for our finding only one adult female in the tree holes. Of the examples of *pollicaris* obtained in the Larut Hills around the turn of the century, only one was taken from other than a tree hole; it was found in a crevice in a rockery of a house at 4513 ft (Butler 1904). Although the botanical collectors on the G. Benom expedition were asked to be on the look out for frogs in the tree crown they did not report seeing any: nevertheless I believe that there is a distinct possibility that careful inspection of high branches and foliage might disclose the full life history and habits of this species.

The Bornean species of *Metaphrynella* has also been found in tree holes, and little apparently is known of its life history except that males call from April to August and a gravid female was found in June (Inger 1966). The gravid female of *pollicaris* was obtained in March.

Variation: In the males there is a marked size variation associated with altitude, individuals from 2950 to 4000 ft varying from 29 to 33 mm in body size while those obtained at 5500 to 6250 ft are between 35 and 40 mm. No other morphological differences in these populations have been found.

Only one adult female *pollicaris* being available it is impossible to be certain whether there is a constant sexual difference in the length of the pollex. However in the single female the tip of the pollex does not project beyond the distal edge of the subarticular tubercle of the first finger whereas in males the tip extends well beyond and in some individuals as much as 3/4 the length of the tubercle.

Colour in life: In most individuals the dorsal pattern is obscure but in some specimens there is an indication of a dark chocolate brown hour-glass shape which begins between the eyes as a broad band, widens on the mid dorsum and becomes more constricted in the sacral region. The most constant feature of the pattern is a dark patch over the anus which is surrounded by a broad light area. Across the femur, distal to this light area, are alternate dark brown and light stripes which do not encircle the thigh but peter out on the posterior edge of the thigh. Tibia, tarsus and foot crossbarred; heel invariably cream.

RANGE: W. Malaysia.

Microhyla annectans Boulenger

Microhyla annectans Boulenger 1900 : 188

MATERIAL: BM 1967.2671–77 (2 ♀, 5 ♂).

HABITAT: Four of the Benom samples were found at night in a small water-filled artificial depression on the forest floor close by camp 4 (5000 ft). They were lying motionless and spread eagled on the water's surface, resembled dead leaves and made no attempt to dive or swim away when disturbed, unlike individuals obtained by Butler in the Larut Hills (Butler 1904). Other specimens were on the peaty soil of the trail close to a similar pool. One example which was on a fallen palm leaf flattened itself when disturbed. The holes had been excavated three days previously in the hope of water seepage from the ground or rain filling them and attracting frogs to them but although the holes soon filled with water and the pools were regularly inspected no frogs were seen until the third and last day spent at the camp. Butler (1904) obtained the syntypes of *annectans* at the margin of a small pond in jungle on the Larut Hills at about 4000 ft, in association with *M. butleri*. He caught nine examples and comments that he 'could easily have obtained many more. When disturbed they at once jumped into the water usually rising with eyes above the surface a few seconds later.'

COLOUR IN LIFE. The upper surfaces of the frogs closely resemble the forest litter of peat and reddish fallen leaves. The dorsum is a rich red-brown or almost a claret colour and the snout is a lighter brown. The symmetrical dorsal patch and the spots and blotches on the flanks, on each side of the vent and on the limbs are a rich dark chocolate brown. The belly is mottled white and black. The ground colour of the upper surfaces is similar to that of *Leptobrachium gracile* found in the same area. All the examples have an oblique whitish line from below the eye to the jaw angle but in some specimens this line continues almost to the axilla as a series of white spots. All have a prominent black patch extending from above the shoulder almost to the groin which is bordered above by a thin white line. On the inside of the upper leg are equally prominent dark patches which extend to the knee. Dark areas are also present on the heel, as black spots on each side of the vent and as crossbars on the femur and tibia. In two individuals the sacral dark bar is reduced to two dark spots or ocelli lying on either side of the vertebral region. None of the Benom series nor the types has a black labial spot (see also taxonomic notes). There appears to be no sexual dichromatism.

Taxonomic notes: The 'adult Malayan male BM 1928.11.12.1' to which Inger (1966) referred in his discussion of *annectans* not only hails from Thailand but differs in several respects from the syntypes of *annectans* and I believe has been incorrectly assigned to this species. The canthus is feebly defined and the loreal region is more oblique than in *annectans*. The third finger length is considerably less than the distance from the tip of the snout to the pupil, in fact is equivalent to snout tip to the anterior border of the eye. In *annectans* the internarial distance equals the length of the fourth finger, whilst in BM 1928.11.12.1 it is twice the length of the fourth finger. The webbing on the toes is less extensive than in *annectans* and on the external aspect of the third toe two phalanges are free whilst the fourth toe has three phalanges free from web on both inner and outer aspects and the fifth toe has almost two free phalanges. Furthermore the snout to vent length (20 mm) is well outside the size range of adult male *annectans* (14·5–15·4 mm). The specimen was collected by Malcolm Smith but has been labelled as having been obtained in Perak. Reference however to Smith's field notebooks indicates that it was in fact collected in January 1916 at Patuju and Smith (1916 & 1930) refers to this individual and states that Patiju (sic) is a state about 60 kms north of the Isthmus of Kra (now Chumphon according to Taylor (1962)). In 1928, but shortly before Smith's specimen was incorporated into the British Museum, Parker published his review of the genus *Microhyla* and, based on Smith's (1916) Patuju record, included Peninsular Siam in the distribution of *M. annectans*. He further incorporated in his description of the species the unusual features of the Patuju specimen that had been mentioned by Smith (1916), namely the black labial spots, black oblique streaks from the eyes to the axillae and the thin light vertebral line, all of which are absent from the syntypes as well as from the G. Benom series, and in 1934 he again modified the description of the syntypes to include the Patuju individual although by this time the specimen was masquerading as a Perak example and is listed as such by Parker. I have also examined 27 specimens from the Field Museum Chicago collections that were obtained in the 3rd and 4th divisions of Sarawak and had been tentatively assigned to *M. annectans*. They differ so radically from the syntypes and from the Benom sample in the development of the fingers that I suspect more than geographical variation is involved and that they almost certainly should be recognized as belonging to a separate taxon. As Inger (1966) has pointed out, Bornean '*annectans*' have no free first finger whereas in the Malayan examples and syntypes the length of the first finger, measured from its tip to the base of the palmar tubercle is equivalent to the distance from the middle of the naris at least as far as the anterior border of the eye. But not only is there reduction in the length of the first finger. Whereas in Malayan material the internarial distance equals the length of the 4th finger, in the Sarawak '*annectans*' it is 1½–2 times the length of the 4th finger. The 3rd finger measured from its tip to the base of the proximal subarticular tubercle (at junction with 4th finger) is relatively shorter than in Malayan *annectans* and is equivalent to the distance from the tip of the snout to the anterior border of the eye (middle of the eye in *annectans*). In the description of Bornean '*annectans*' given by Inger (1966) it is stated that the fourth toe has two phalanges free from web but in the series of

Sarawak individuals that I have seen the web usually extends to the base of the disk or at least to beyond the distal edge of the distal subarticular tubercle. This is a considerably fuller web than is developed in the *annectans* syntypes and in the G. Benom series.

RANGE: W. Malaysia.

Microhyla berdmorei Blyth

Engystoma (?) *berdmorei* Blyth 1856 : 720.

MATERIAL: BM 1967.2678–9 (2 gravid ♀).

HABITAT: On disused logging track to K. Damak by banana stands in disturbed forest ca 600 ft.

COLOUR IN LIFE: Pink/grey dorsum with dark mushroom scapular and sacral marks and cross bands on hind limbs. Flanks, belly and undersurface of thighs sulphur yellow, chest creamy yellow, throat grey/brown speckled with dark brown.

REMARKS: In the larger of the two specimens (S–V 30·2 mm) the wartiness of the skin is more or less confined to the upper surface of the head and to the anal region, whereas in the smaller individual (S-V 28·2 mm) the entire dorsal surfaces of head, body and limbs are warty and the granulation extends beyond the vent to the posterior portion of the belly.

RANGE: Burma, Thailand, Cambodia, W. Malaysia and Sumatra.

Microhyla butleri Boulenger

Microhyla butleri Boulenger 1900 : 188.

MATERIAL: BM 1967.2680–81 (1 ♂, 1 ♀).

HABITAT: The male 2681, was found at 600 ft, at night about one mile from Base camp towards K. Damak after heavy rain, on a low bush by the side of the logging track where *Microhyla heymonsi* was breeding in puddles. Nearby and among the stands of banana *Rhacophorus nigropalmatus* was collected. The female was brought in by one of the mammalogists and no precise habitat details are available.

COLOUR IN LIFE: The large dorsal mark which Parker (1934) described in detail fits the Benom specimens admirably but is not light edged. The oblique light stripe from behind the eye to the axilla is prominent and bordering the stripe behind is a dark brown triangular spot. No reddish colouration of the tubercles was noted.

RANGE: Burma, Thailand, S. China, Vietnam, Hainan, W. Malaysia, Singapore.

Microhyla heymonsi Vogt

Microhyla heymonsi Vogt 1911 : 181.

Material: BM 1967.2682–94 (7 ♂, 6 ♀).

Habitat: Close to rain puddles and small low plants on disused logging track to K. Damak, 600–700 ft, flanked by recent secondary growth and banana stands in rain forest.

Call: k-r-r-i-c-k, k-r-r-i-c-k repeated at regular intervals.

Remarks: The fine light vertebral line which Parker (1934) found to be generally present in examples of *heymonsi* is clearly discernible in all the individuals in this series; furthermore each has a small dark spot on each side of the line on the middle of the back. More than half the sample, males as well as females, have an additional pair of similar spots between the shoulders. No other dorsal spots are present. In morphology and in other aspects of colour pattern the Benom series agree fully with Parker's detailed description of the species.

Range: From Thailand through Vietnam to S. China, also W. Malaysia, Singapore and Sumatra.

Phrynella pulchra Boulenger

Phrynella pulchra Boulenger 1887 : 346.

Material: BM 1967.2720–24 (1 ♀, 4 ♂).

Habitat: The series emanated from diverse microhabitats: rim of the washing-up bowl on the mess floor, a porter's bed, groove in the trunk of a felled tree, on the muddy logging track. All were found at night during or after heavy and prolonged rains at Base camp, 700 ft.

Colour in life: The general colour of the upper surfaces of four specimens was grey and black but one specimen (2724) was grass green on the posterior half of the body. The belly of all five was vivid vermilion and this colour continued on to the undersurfaces of the hind limbs and formed a broad supra-anal band and bright lumbar patches on the flanks. The throats of both the males and the females were black and the thoracic region speckled black.

Range: W. Malaysia, Sumatra, Mentawei Is.

Family **PELOBATIDAE**

Leptobrachium gracile Günther

Leptobrachium gracile Günther 1872 : 598.

Material: BM 1967.2297–8 (1 gravid ♀, 1 ♂). BM 1967.2299–2308 (developmental series at early and late metamorphic stages).

Habitat: The two adults taken close to camp 4 (5000 ft) were found at night on plants about 2 ft above the forest floor. The series of nine larvae were obtained in a clear, almost still pool in a narrow, slow moving stream (ca 3430 ft) in the valley below camp 3. The pool, with fine gravel bottom and about 2 ft deep, was surrounded by large stones and boulders among which the tadpoles darted when a torchlight was shone on the water's surface. On the stream's bank, alongside the pool and on a low broad-leaved plant by a boulder, specimen 2299 (in which the mouth is adult in form and the tail partially resorbed) was taken.

Colour in life: The adults were a mottled dull claret with a dull coral red on the upper arms. The tubercles on the upper surfaces of body and limbs were bright orange red, those on the flanks and hind limbs being wholly or partly encircled with dark brown. The iris, canthal edge, rim of eyelid, supratympanic fold and the flat round glands on each side of the thorax near the axillae were also orange-red. When alive the larvae were uniform reddish-brown.

Remarks: The adults (♀ S–V 47·2 mm: ♂ S–V 33·8 mm) agree favourably with Boulenger's (1908) and Inger's (1966) descriptions of the species except that in the Benom individuals the interorbital area is broader not narrower than the upper eyelid. The premetamorphic larvae have the typical pelobatid mouthparts and all have short rows of labial teeth, the dental formula being $\frac{\mathrm{I}:\ 2\text{–}2}{3\text{–}3:\ \mathrm{I}}$ in six specimens. In the three other larvae the formulae are $\frac{\mathrm{I}:\ 1\text{–}3,}{3\text{–}3:\ \mathrm{I}}$ $\frac{\mathrm{I}:\ 2\text{–}2,}{2\text{–}2:\ \mathrm{I}}$ $\frac{\mathrm{I}:\ 2\text{–}2.}{3\text{–}3:\ \mathrm{I}}$ These counts are within the variation observed by Inger (1966) in Bornean samples of *gracile*. However total lengths of the Benom larvae differ markedly from those in Inger's series and there apparently is a further difference in tail shape. The Bornean larvae varied between 25·0 and 47·0 mm in total length and the tail tips were described by Inger as rounded, while the Benom larvae with undamaged tails are 59·1–78·2 mm (M 69·7 mm) and their tails taper rapidly to a sharp point. The larvae of *L. heteropus*, which is the only other species of *Leptobrachium* so far found on Benom, are not known. In total length the Benom specimens are similar to *L. hasselti* but there the similarity ends for in proportions and in other characters there are many differences between the larvae of the two species. Larvae of *hasselti* are much less streamlined and fish-like in appearance, are heavily spotted all over, have a convex, dorsal fin that is as deep as the caudal muscle, except in the proximal third of the tail, and have a bulbous head and body that in width is only a little more than two-thirds of its length and in length is 1/2–2/3 the total length; in depth the head and body are considerably greater than the tail. *L. gracile*, on the other hand, has an elongate tadpole with head and body only 1/3 of the total length and in depth much less than the depth of the tail. The tadpoles of all other Malayan species of *Leptobrachium* are either much smaller or in pattern and in mouthparts differ from the Benom material. Although *L. pelodytoides* tadpoles in proportions are similar, in total length (63 mm) and in pattern (speckled and spotted with black) they differ from the G. Benom series.

Range: W. Malaysia and Borneo.

Leptobrachium heteropus Boulenger

Leptobrachium heteropus Boulenger 1900 : 186.

MATERIAL: BM 1967.2309–17 (9 ♂).

HABITAT: All the examples except one were found on leaves of small plants, no more than 1 ft from ground, in or near a shallow, narrow, slow moving stream in the valley below camp 2, approximately 1650 ft. The exception was found at a similar height from the ground calling from a tree stump in wet clay in the stream bed.

SECONDARY SEX CHARACTERS: The males have small, round, paired openings to the vocal sac on a level with the jaw angles and close to them. The gular skin is puckered. There are no nuptial pads or pectoral glands.

RANGE: Previously known only from the holotype obtained in the Larut Hills, Perak at 3500 ft although a few specimens obtained at Taman Negara, Pahang that are in the University of Malaya collections have been tentatively assigned to this species.

Megophrys aceras (Boulenger)

Megalophrys montana var *aceras* Boulenger 1903 : 132.

MATERIAL: BM 1967.2325–27 (2 ♀, 1 ♂).

HABITAT: The females were found at night on the peaty ground of the forest floor in the boulder strewn area of the ridge at 3650 ft, one specimen being at the back of the overhang of a large boulder. The male was taken on a boulder in the forest near to the stream in the valley below camp 3 at ca 3400 ft.

CALL: A single note, like that from a tuba, heard at night in the area in which the male *aceras* was found, may be the call of this species. The only other species of amphibian collected in the area were *Philautus aurifasciatus*, *Amolops larutensis*, *Leptobrachium gracile*, *Bufo asper* and *Ansonia ? tiomanica*.

COLOUR IN LIFE: The most striking feature of this species is the vivid vermilion of the iris and insides of the thighs. The dorsum is steel grey, paler on top of the head except for a large black triangular mark on the occiput and eyelids. There is a somewhat obscure, dark spot on the middle of the shoulders at the apex of the V-shaped fold. Additional black spots are present on the flanks, especially in the male, and in all three examples some black streaks or coalescing spots occur along the dorsolateral fold. Undersurface of the upper eyelid is spotted black. Black spots along the back of the upper arm, below the elbow and under the wrist. Narrow, oblique dark crossbars on the hind limb; dark patches on the chest, along the midline of the throat, below and behind the axilla; venter otherwise mottled grey and white. A round, black spot on the knee and 3–4 black spots on the hind edge of the tibia. Inside of the heel, undersurface of the tarsus and metatarsus black. Entire posterior surface of the thigh with very fine, white speckling but a black area over the vent extends along the thigh as a broad band and 2/3 along the thigh in the middle of this dark, thigh band is a single white spot. A white, pectoral conical tubercle on each side.

SECONDARY SEX CHARACTERS: Male *aceras* examined by Smith (1926) had a snout–vent length 49–57 mm. The male syntype and the G. Benom male, both of which are sexually mature, are 48·1 and 51·1 mm respectively. Smith's two females measured 75 and 83 mm; the two females in the G. Benom collection, both of which contain ripe, unpigmented eggs, have a body length of 82·2 and 85·6 mm. In the G. Benom male the entire dorsum, upper surfaces of the limbs, the sides of the head, the lips and the chin are beset with small, white horn-tipped tubercles. The mediodorsal surface of the basal half of the first finger bears a dark nuptial pad and there is also a small, roundish group of asperities on the basal knuckle of the second finger. A median, subgular, internal vocal sac is present; it opens by paired, round openings which lie near but a little behind the commissure of the jaws.

REMARKS: I find the following characters to be reliable for separating *M. aceras* from *M. monticola nasuta*:

1. On the back a single pair of curved, longitudinal folds that splay out on the shoulder region and end on the haunches about 7/8 of the way along the trunk. The folds start on or just above the supratympanic folds at the level of, or a little behind the posterior rim of the tympanum.
2. Absence of dermal appendage on the snout and at jaw commissure.
3. Dermal projections from the edge of the upper eyelids either absent or small (up to 2 mm).
4. Inner metatarsal tubercle 4/5 length of first toe.
5. Absence of transverse occipital fold.
6. Presence of a V-shaped or hourglass-shaped ridge or line of tubercles between the shoulders.
7. Width of head only very slightly greater than its length (less than 1¼ times).
8. Tympanum clearly discernible, its diameter ½ internarial distance.
9. Loreal region vertical, lips not flaring.
10. Iris vermilion in life.

RANGE: Peninsular Thailand and Malaya.

Megophrys monticola nasuta (Schlegel)

Ceratophryne nasuta Schlegel 1858 : 57.

MATERIAL: BM 1967.2318–24 (1 ♀, 5 ♂, 1 juvenile).

HABITAT: Most of the examples were found at night on the forest floor among dead leaves in areas close to streams, between 600 and 1650 ft. One adult male was found at night sitting upright in the stream by fallen leaves, between boulders, just below the small waterfall at 1650 ft in the valley below camp 3.

COLOUR IN LIFE: Above tan or chocolate brown, the middle of the trunk from behind the orbits to the vent a darker shade, this area being bordered anteriorly by a wide angled 'V'. One or two dark brown transverse stripes across the top of the head. A dark brown, white bordered loreal patch and an oblique dark chocolate brown, sometimes white-edged stripe from below the posterior half of the eye to the upper lip were constantly present. A few, small, round, conical, almost black tubercles irregularly scattered over the back. Across the vent a dark brown area with median constriction. Throat and chest usually chocolate brown or grey-brown mottled with darker brown and with a dark, median band; belly marbled brown and cream. A dark brown spot under forearm and dark patches under wrist and on knee; under surfaces of tarsus and metatarsus dark chocolate brown. Iris medium brown.

REMARKS: Inger (1954) has given an excellent and detailed description of *monticola* and an account on geographic variation and the characteristics of *monticola nasuta*. See also remarks under *M. aceras*.

RANGE: Malay Peninsula, Sumatra, Natuna and Borneo (Inger 1954).

Family **RANIDAE**

Amolops larutensis (Boulenger)

Rana larutensis Boulenger 1899 : 273.

MATERIAL: BM 1967.2328–57, 1967.2489–91 (7 ♀, 17 ♂, 9 immature).

HABITAT: 700–5000 ft in disturbed rainforest and in primary forest. The species was common at night on large, wet boulders in the fast-flowing stream at Base camp but became progressively rarer at higher altitudes, only two examples being found at 3400 ft and one at 5000 ft, but these occupying a similar niche to those in the lowlands.

RANGE: W. Malaysia.

Rana blythi (Boulenger)

Rana macrodon var. *blythi* Boulenger 1920 : 43.

MATERIAL: BM 1967.2423–34, 1967.2435, 1967.2500–01 (6 ♀, 5 ♂, 4 juveniles).

HABITAT: 500-1600 ft in both narrow and wide, clear streams among virgin forest, generally on stones or on the banks.

REMARKS: Females vary in body size from 71·7 to 147·5 mm, five that have well developed ovarian eggs and convoluted oviducts ranging from 71·7 to 81·6 mm. The five males measure from 83·7 to 98·2 mm. In head proportions and in tibia length, as well as in other characters, they agree closely with the proportions given by Inger (1966) for a series of Malayan *blythi*. In the G. Benom specimens the head width to snout–vent ratio is 0·337–0·374 (♀♀), 0·366–0·386 (♂♂), head length to snout–vent 0·383-0·421 (♀♀), 0·443–0·477 (♂♂) and the tibia to snout–vent ratio is 0·546–0·582 (♀♀), 0·521–0·557 (♂♂). They further agree with Inger's Malayan sample in lacking a dark, horizontal loreal stripe. Four individuals have a broad mid-dorsal light band, one has only a thin, light line. Inger states that male *blythi* lack vocal sacs, nuptial pads and any other distinctive (secondary sex) structures but in the G. Benom sample the bony mandibular projections are considerably better developed in males.

RANGE: W. Malaysia, Singapore, Sumatra and Borneo.

Rana chalconota raniceps (Peters)

Polypedetes raniceps Peters 1871 : 580.

MATERIAL: BM 1967.2436–59 (20 ♂, 4 ♀).

HABITAT: The females were found on stones and boulders splashed by spray in the stream at Base camp (700 ft) and also among bank-side vegetation. All the males were around the quiet backwater to the stream, either on the muddy bank or sitting on branches of trees overhanging the water (see also *Rana signata*).

COLOUR IN LIFE: Dorsum either grass green or yellow-green and usually with brown spots. Posterior aspect of thighs pale buff coloured. Upper lip creamy yellow, especially on posterior half, the light colour extending to the edge of the lip, as is usual in Bornean and Malayan populations (Inger 1966).

REMARKS: The entire series was collected between the 18th and 25th February when females contain enlarged pigmented ova and males were calling. In Borneo the breeding period extends at least from April to September (Inger 1966). In eight of the adult males the nuptial pad covers the medio-dorsal area of the base of the first finger, in the remainder the pad is less well developed and is partially or wholly divided into two.

RANGE: The subspecies *raniceps* occurs in W. Malaysia and Borneo, and possibly also Sumatra and peninsular Thailand (Inger 1966).

Rana hosii Boulenger

Rana hosii Boulenger 1891 : 290.

MATERIAL: BM 1967.2460–80, 1967.2481–88 (7 ♀, 21 ♂).

HABITAT: All the specimens were obtained from boulders in the clear, fast flowing stream at Base camp, 700 ft, or from its banks and overhanging branches.

COLOUR IN LIFE: The colour was very variable, the dorsum and flanks of some specimens being uniform grass green, of others olive green or green spotted with brown or brown spotted with green. The backs of the thighs were marbled dark green and brown; the tympanic area and the dorso-lateral fold dark brown. The upper lip and the spot at the jaw angle were yellow and the iris golden yellow.

RANGE: Thailand, W. Malaysia, Sumatra, Java and Borneo.

Rana laticeps Boulenger

Rana laticeps Boulenger 1882 : 20.

MATERIAL: BM 1967.2390–2420 (males, females, halfgrown & juveniles.

HABITAT: All specimens were obtained in aquatic situations under forest from 600–3400 ft. Examples would invariably be found at night in quiet shallow pools at the edges of streams, lurking between stones or under wet fallen leaves and twigs.

Occasional individuals, usually females or immature specimens, were taken from crevices in rotten logs, from the clay banks of streams or from the gravelly stream bed. When disturbed *laticeps* either rapidly swims away or remains motionless, if in water lying with only the eyes protruding from the surface. The wide, fast-flowing stream at Base camp harboured this species only in a restricted area where the current slackened at the margins and shallow (less than 3″ deep) gravel-based pools formed. At higher elevations examples were found at night in rock pools in a steep and exceedingly wet area after prolonged rains, about 20 yds from a fall of water in a narrow stream in the valley below camp 2.

CALL: The male calls from water, its head and upper jaw above the surface. The gular skin inflates and pulsates as the soft, melodious gargling sound, which goes up the scale, is uttered. Since no vocal sacs are present in this species it is presumed that when the male calls air that is being shunted to and fro to the buccal cavity causes distention of the loose plicate lining to the floor of the mouth and thus inflation of the gular skin. The mating call was recorded and males responded readily to the play back.

COLOUR IN LIFE: The corrugated upper surfaces were generally orange-brown with darker brown interorbital bar, paired blotches on the middle of the back, lip spots, diagonal temporal band and crossbands on the limbs. Gular region mottled brown and white in females and immature individuals, paler and more greyish in males; belly grey/white. Undersurfaces of hind limbs in all but juvenile frogs vivid orange. None of the examples had yellow on the chest, belly or ventral surfaces of the legs as reported by Inger (1966) as occurring in Bornean examples.

REMARKS: Eleven females with enlarged ova range in size from 36·9–42·0 mm (M = 39·7). Males in which the testes are apparently ripe and the mandibular odontoids well developed and sharp vary from 34·7–45·4 (M = 41·9 N9); none has any trace of a nuptial thumb pad.

RANGE: Assam to Thailand, W. Malaysia, Borneo (Sarawak).

Rana limnocharis limnocharis Wiegmann

Rana limnocharis Wiegmann in Meyen 1835 : 255.

MATERIAL: BM 1967.2492–99, 1967.2578 (3 ♀, 6 ♂).

HABITAT: This species was found only in the cleared areas at Base camp, 700 ft.

RANGE: From Ceylon and India to Taiwan and Japan, also W. Malaysia, Singapore, Sumatra, Java, Borneo and the Lesser Sundas as far as Flores.

Rana luctuosa (Peters)

Limnodytes luctuosus Peters 1871 : 579.

MATERIAL: BM 1967.2371–77 (4 ♂, 3 gravid ♀, 1 larva).

HABITAT: All the examples were taken in or near flooded ruts on the logging tracks in disturbed forest between 700 and 1950 ft.

Colour in life: Head and back rich chocolate brown bordered by narrow cream dorso-lateral line which extends from tip of snout along canthus, edge of upper eyelid to above the vent. Sides of body black. Limbs crossbarred pale grey and black; back of thighs black spotted with white. Ventral surfaces light grey. Flower's (1896) colour plate of this species closely resembles the Benom specimens.

Remarks: The size of the males (S–V 39·3–42·9 mm) and the absence of stripes on the undersurfaces of the limbs of this Benom series confirm Inger's (1966) statement that Malayan examples of *luctuosa* are not only smaller but lack the limb pattern of Bornean populations. The four males appear to be sexually mature and have well developed humeral glands which vary in length from 2·9–3·9 mm. The females with enlarged unpigmented ova measure 46·5, 47·9 and 51·7 mm.

The dental formula in the larva, which has hind limbs well developed, is $\frac{5-5}{1-1:\mathrm{III}}$. The division of the outermost rows on the upper lip may be due to damage.

Range: W. Malaysia (Penang, Perak, Pahang and Selangor States), Borneo (Sarawak and W. Sabah).

Rana miopus Boulenger

Rana miopus Boulenger 1918 : 11.

Material: BM 1967.2421–2 (2 gravid ♀).

Habitat: Both frogs were found on the main logging track within ½ mile of Base camp at a point where there is considerable secondary growth and wild bananas flanking the track at ca 750 ft.

Colour in life: Upper surfaces orange-red, the dorso-lateral folds somewhat lighter. The post tympanic diagonal band, the spots in the groin as well as the streaks on the haunches adjacent to the dorso-lateral folds black. Back of thighs marbled black and grey. Legs with grey brown crossbars. Diagonal streaks across back also grey-brown.

Range: Known only from the type locality in the southern part of peninsular Thailand, from one specimen obtained in the Chikus Forest Reserve, Perak and from individuals taken in Kelantan and in north, central and southeast Pahang, W. Malaysia.

Rana nicobariensis (Stoliczka)

Hylorana nicobariensis Stoliczka 1870 : 150.

Material: BM 1967.2725 (1 ♀), BM 1967.2389 (1 juvenile).

Habitat: The female was collected at Base camp, 700 ft, in the large camp clearing in disturbed rainforest, while the juvenile was found on the wide track leading to the camp.

Colour in life: No colour notes were made on the adult. Since at the time the frog was collected it was assumed to be another *Rana chalconota* it is likely that the colour in life was similar in the two species. The upper lip of the juvenile pale green; iris reddish brown.

REMARKS: Although this species superficially resembles *Rana chalconota raniceps*, in Benom individuals there is a marked difference in the size and proportions of gravid females, the *nicobariensis* specimen measuring only 46·8 mm in body length while the four adult females of *chalconota* (obtained within 200 yds of the *nicobariensis*) varied from 49·6 to 55·7 mm, average 52·9 mm. Inger (1966) however reports no size difference between the species in Bornean populations, the size ranges for long series of females being 46·5–53·2 mm in *nicobariensis* and 46·0–59·4 mm in *raniceps* with means 50·11 ± 0·44 and 50·68 ± 0·51 mm respectively. With only one example of *nicobariensis* it is unwise to draw any definite conclusions on Pahang populations. The most reliable distinguishing feature between the two species is the considerably less webbing in *nicobariensis* (see figures in Inger 1966).

RANGE: Peninsular parts of Burma and Thailand, W. Malaysia, Sumatra, Java, Borneo to Bali and Philippines (Palawan).

Rana plicatella Stoliczka

Rana plicatella Stoliczka 1873 : 116.

MATERIAL: BM 1967.2362–70 (2 ♂, 7 juveniles).

HABITAT: One of the adult males was found on the bank above a soft muddy area with standing water, close to a rivulet that had little current and joined the left bank of the River Kerau tributary 200 yards further on. The other male was said to have come from the same area, about 300 yds downstream from Base camp and at approximately 700 ft.

COLOUR IN LIFE: Upper surfaces mid-chestnut brown with darker brown glandular ridges and with dark crossbars on the limbs. One adult with a cream vertebral band. Throat white, chest and belly sulphur yellow, undersurfaces of hind limbs yellow speckled with brown.

RANGE: Thailand south of Yala Province, W. Malaysia.

Rana signata signata (Günther)

Polypedetes signata Günther 1872 : 600.

MATERIAL: BM 1967.2378–88 (10 ♂, 1 ♀).

HABITAT: On Benom *Rana signata* seems to be limited to the lowland rainforest at 700 ft where it occupies a very restricted niche by secondary growth close to the fast flowing tributary of the River Kerau. A distinct preference was shown for a steep mud bank above a still backwater. The backwater, approximately 20 × 12 ft with clear water and a soft mud base, was about 3 ft deep and overhung by branches. At one end where there were large boulders sprayed by the force of the stream *Amolops larutensis* occurred and at the base of the boulders, close to the water, *Bufo asper* was common. The males of *signata* were always on the bank 6–12″ above the water calling from the ground but exceedingly difficult to locate by their call as they seem to throw their voices. The call is like a laugh, ha-ha-ha-ha-ha repeated quickly and quietly. Higher on the bank and closer to the forest litter and bases of trees and bushes or on branches of the trees overhanging the backwater males of *Rana chalconota* occurred and I agree with Inger (1969) that *chalconota* has stronger arboreal tendencies than *signata* for nowhere did I witness any evidence of *signata* having even partial arboreal habits. The only adult female that was obtained was collected by a porter at night from the 'stream area at Base camp'; no further data are available.

COLOUR IN LIFE: Dark brown or blackish on upper surfaces with pale apple green or cream spots and blotches on the dorsum and backs of thighs. The limbs with orange coloured cross bars, the bars often broken up into spots. From the tip of the snout, along the canthus and the edge of the upper eyelid an orange line extended dorso-laterally to the groin. In all the examples there is at some point a break in the dorso-lateral line.

SECONDARY SEX CHARACTERS: Similar to those described by Inger (1966) for Bornean populations and no geographical variation in size seems to occur.

RANGE: Peninsular parts of Thailand, W. Malaysia (Pahang and Kelantan), Sumatra and Borneo.

Rana tweediei Smith

Rana tweediei Smith 1935 : 62.

MATERIAL: BM 1967.2358–61 (2♀, 1 halfgrown ♀, 1 ♂).

HABITAT: All were obtained in muddy areas under forest close to small streams, between 700 and 2500 ft.

COLOUR IN LIFE: Dorsum grey and dark brown, the grey being more or less confined to a broad band between the front halves of the upper eyelids, to paravertebral longitudinal streaks, to the sides of the body, to limb cross bars and to vertical streaks on the upper lips. The rest of the upper surfaces were brown, the dorso-lateral glandular folds and interorbital bar rather darker brown. Belly lemon, undersurfaces of thighs and tibia vivid orange, throat white, mottled with brown. A vertebral line similar to that present in the type occurs in the male but is absent in all the females. In life this line was whitish, not yellow as in Smith's (1935) description of the type. The sexes do not differ in their colours in life.

REMARKS. The two adult ♀♀, S–V 39·9 and 41·8 mm, have enlarged ova with heavily pigmented poles. They are apparently the first females of this species to have been collected. The sexually mature ♂, S–V 41·1 mm, has, like the type, no secondary sexual characters. No size difference in the sexes occurs and the only external feature that may distinguish them is the male's vertebral band, the fine white line on the hind limbs which in the Benom specimen is restricted to the heel and tarsus, and a greater number of tubercles on the back and limbs (see below).

The series has been compared with the holotype and paratypes and agreement is close. Although Smith mentioned the presence of tubercles on the upper eyelids of the holotype he omitted any reference to similar white tipped tubercles above the vent, on the haunches and especially on the hind limbs; such tubercles occur on these areas in both the type series and in all the Benom material but are less well developed in the females. Additional characters omitted by Smith but present in all examples are a feeble transverse groove on the head, immediately behind the dark interorbital bar, and one to three white spots along under-surface of forearm.

RANGE: Previously known only from the type series (near R. Yum, Headwaters of R. Plus, E. Perak, W. Malaysia).

Family **RHACOPHORIDAE**

Philautus aurifasciatus (Schlegel)

Hyla aurifasciatus Schlegel 1837 : 27.

MATERIAL: BM 1967.2620–57 (10 ♀, 25 ♂, 3 juveniles).

HABITAT: This species was seen and heard only between 3400 and 5000 ft. Specimens were collected mostly at night. They were never more than 5 ft from the forest floor, generally on the leaves of small palms or other low plants and bushes. In the valley below camp 3 it was the most common species especially on and at the sides of the wide boulder strewn stream bed.

COLOUR IN LIFE: There was marked individual variation both in pattern and in the shades of brown on the dorsum. A dark chocolate brown interorbital bar was generally evident. Some individuals have a bold dark brown H-shaped mark on the back and on each side of the cross bar of the H a roundish dark brown blotch. Other individuals have a khaki coloured mid dorsal band which extends from the tip of the snout, covers the entire upper surface of the head, narrows behind the eyes and passes back to the vent. A thin, dark vertebral line or a broader, dark brown vertebral stripe may also be present. Yet other individuals have only remnants of the H-shaped dorsal pattern, usually a pair of dorsolateral dark streaks and occasionally in addition the anterior dark blotch. The sides of the body and head were reddish brown with light spots on the haunches, groin, front and back of the thighs and on the undersurface of the tibia. Upper surfaces of the hind limbs crossbarred in dark brown. Ventral surfaces mottled greyish brown, especially on the throat.

REMARKS. These specimens have been compared with the syntypes of *Ixalus petersi* Boulenger, considered by Inger (1966) to be conspecific with *aurifasciatus*, and with the syntypes of *Ixalus larutensis* Boulenger which Smith (1930) placed in the synonymy of *I. petersi*. It is not clear from Inger's account of *aurifasciatus* whether he accepted Smith's 1930 concept of *Philautus petersi*. Inger (1966) concluded that a conically tipped snout in *aurifasciatus* is a highly variable character that may or may not be developed in material from Borneo and Java, even in specimens from the same locality. In the G. Benom examples, the conical tip is more often present and better developed in mature females than in males. A lingual papilla is generally present in both sexes. The outer edge of the fifth metatarsal and of the fifth toe bear a narrow crenulated fringe.

SECONDARY SEX CHARACTERS: The Malayan examples are slightly larger at sexual maturity than the Bornean populations reported on by Inger (1966). The seven gravid females in the G. Benom material vary in body length 31·0–36·7 mm (average 33·6) and 25 males that have a nuptial pad developed measure 20·6–26·2 (average 23·8). The means of the body lengths of Bornean adults are 29·85 (♀♀) and 21·78 (♂♂).

RANGE: From Thailand and Cambodia to Java, Borneo and the Philippines (Inger 1966).

Philautus vermiculatus Boulenger

Ixalus vermiculatus Boulenger 1900 : 187.

MATERIAL: BM 1967.2658–61 (4 ♂).

HABITAT: On rattan and branches of trees in neighbourhood of camp 4 at 5000 ft. This species calls only from high up in the trees. The call crack-crack-crack-crack was heard at several points but the frogs were difficult to locate and collect.

COLOUR IN LIFE: The dorsum of two adult specimens was brown and fawn, the forearm, belly, thighs and flanks golden yellow or orange. The thighs of one individual were spotted yellow and brown. The smallest specimen had a green dorsum with an irregular brown hour-glass pattern and a yellowish throat. Iris silver-grey.

REMARKS: This species was described as having a smooth dorsum (Boulenger 1900b) but examination of the type and of the type of *Ixalus brevipes* Blgr. with which it was synomymized shows that both have small warts scattered over the upper surfaces, especially on top of the snout, above the supratympanic folds and on the heels. The G. Benom specimens also have warts, these being especially prominent on the upper eyelids, shoulders and tibias. Additional distinguishing features are the strongly oblique lores and flaring lips, the curved canthus, and the internarial distance greater than the distance between the naris and the anterior border of the eye and between two and three times the tympanic diameter (in adults twice). In the type as well as in the G. Benom examples the diameter of the third finger disk is consistently greater than the tympanic diameter and not subequal as stated by Boulenger (1900b).

The four Benom examples vary in pattern from the symmetrical markings typical of *brevipes* (Boulenger 1908) to close vermiculations. A light line between the anterior halves of the upper eyelids and two oblique light lines from below the eye to the upper lip are constant. Pigmentation of the groin and of the front of the thighs is absent.

RANGE: Thailand and W. Malaysia.

Rhacophorus appendiculatus (Günther)

Polypedetes appendiculatus Günther 1858 : 79.

MATERIAL: BM 1967.2503 (1 ♂).

HABITAT: The specimen was found at night 6 ft from the forest floor on a tree in an area of secondary growth at the side of a track close to Base camp at 700 ft.

COLOUR IN LIFE: Dorsum mottled light brown. Thighs pinkish orange on both anterior and posterior surfaces. Throat and belly yellow.

REMARKS: In all characters except snout shape this individual closely resembles the type of *Rhacophorus chaseni* (Smith 1924a) which Inger (1966) considered a synonym of *R. appendiculatus*. Like *chaseni* it has below the vent a pronounced transverse dermal flap with crenulated border interrupted on the midline, and from the heel to the 5th toe and also along the forearm to the 4th finger continuous scalloped fringes. There is a scalloped seam too along the lower edge of the lower jaw. But while there is a small dermal projection at the tip of the snout it is very much less pronounced than in the gravid female holotype of *chaseni*. Additional Malayan examples may show that there is a sexual difference in the development of this appendage. The webbing on the toes of the holotype of *chaseni* does not extend to the disks, as described and shown in pl. 1 fig. 1 (Smith 1924a); instead, on the inner aspect of the second, third and fourth toes the web reaches only the distal subarticular tubercles and in this respect agrees with the G. Benom example.

RANGE: W. Malaysia, Sumatra, Borneo, Philippines.

Rhacophorus colletti Boulenger

Rhacophorus colletti Boulenger 1890 : 36.

MATERIAL: BM 1967.2504 (1 gravid ♀).

HABITAT: The specimen was collected at night on a leaf on the ridge E.S.E. of Base camp at about 800 ft. A *Cyrtodactylus marmoratus* was obtained on the same tree.

COLOUR IN LIFE: Dorsum uniform pinkish brown.

REMARKS: The specimen agrees well with Inger's (1966) excellent description of the species except for the absence on the dorsum of the dark hour glass-shaped figure which apparently is usually present in Bornean and Thai examples.

RANGE: Extreme southern States of Thailand, W. Malaysia (Pahang), Sumatra, Borneo and islands in the South China Sea.

Rhacophorus leucomystax leucomystax (Boie)

Hyla leucomystax Boie in Gravenhorst 1829 : 26.

MATERIAL: BM 1967.2534–77, 1967.2579–89, 1967.2590–619 (27 ♀, 57 ♂, 1 immature).

Habitat: 600–1950 ft in both primary and secondary forest. The species was particularly common on stems of plants up to 7 ft from the ground, in flooded ditches and in temporary pools between 600 and 1700 ft around clearings and in other areas of disturbance associated with logging. Above 1700 ft specimens were found only on bushes flanking the track.

Range: The nominate form occurs from Tenasserim through Thailand to Hainan and northern Vietnam and in W. Malaysia, Singapore, Sumatra, Java, Borneo and the Philippines.

Rhacophorus macrotis Boulenger

Rhacophorus macrotis Boulenger 1891 : 282.

Material: BM 1967.2533 (1 ♂).

Habitat: No information other than 'Base camp area, 700 ft'.

Colour in life: The ground colour of the upper surfaces was brick red, with a pair of darker spots between the eyes forming an interorbital bar interrupted medially; other median dark spots on the back. From behind the eye to the flanks a striking dark, almost black horizontal band which covers the tympanum and tapers slightly behind the arm; the band is bordered below by a cream line. A fine white line extends along the outer edge of the forearm and hand. A fine, white line above the vent; two white tubercles below the vent. Flanks marbled. Hind limbs with dark cross bars above. A prominent dark heel patch. Venter whitish, the belly finely speckled.

Remarks: In the field this specimen was mistaken for *Rhacophorus leucomystax*, two *leucomystax* having a similar brick red dorsum and a somewhat similar appearance, but a closer examination revealed not only that this specimen is much larger than male *leucomystax* (S–V 60·5 mm) but that it has a sharper canthus, more vertical loreal region and more widely flaring lips, less finger webbing and more extensive toe webbing and in other characters too closely resembles *R. macrotis* which was not known to occur in the Malayan peninsula.

Range: W. Malaysia, Sumatra, Borneo, Natuna Is., Philippines (Palawan and Sulu Archipelago).

Rhacophorus nigropalmatus Boulenger

Rhacophorus nigropalmatus Boulenger 1895 : 170.

Material: BM 1967.2505–21 (3 ♀, 14 ♂).

Habitat: On Gunong Benom the habitat and altitudinal distribution of this species closely paralleled those of *Rhacophorus prominanus* and *R. reinwardtii*. All these species were obtained from flooded, muddy ruts and other temporary pools on the main track, as well as from branches overhanging the pools, in forest between 700 and 1650 ft approximately, but *R. nigropalmatus* showed a preference for higher trees, bushes and palms and seem called from greater heights.

Call: A loud, clear, teuk-teuk-teuk-teuk which somewhat resembles the tapping of a woodpecker.

Colour in life: Grass green granular upper surfaces with minute white tubercles and occasionally also large, white blotches on the head and hind limbs. Flanks, inside of thighs and undersurfaces yellow. Finger and toe web jet black except for the distal margins which were yellow finely streaked with black. Upper surfaces of toes 1–4 yellow. Iris white.

Range: Peninsular parts of Thailand, W. Malaysia, Sumatra, Borneo.

Rhacophorus prominanus Smith

Rhacophorus prominanus Smith 1924 : 185.

Material: BM 1967.2530–32 (3 ♂), BM 1967.2662–4 (3 larvae).

Habitat: On branch overhanging puddle in track and in flooded ruts in the track at 800 ft, 1300 ft and 1650 ft.

Colour in life: Upper surfaces of the body and limbs a soft blue-green with small brown spots; belly yellowish. Web between the fingers yellowish, toe web blood red between the 3rd and 4th and 4th and 5th toes. Iris pale buff, heavily streaked with red.

Larvae: Three premetamorphic tadpoles at stages XI–XVII, obtained from a pool on a logging track at ca 900 ft are tentatively assigned to this species. Their size, very broad feet with full web extending to the toe disks suggests that they belong to the *nigropalmatus*, *prominanus*, *reinwardtii* group. Their dental formula, however, does not agree with that given for *nigropalmatus* (Inger 1966) and the unpigmented webbing on the toes makes assignment to *reinwardtii* unlikely. A composite description of the three G. Benom tadpoles is as follows: body ovate, flattened above and below; eyes dorsal, not visible from below; diameter of eye subequal to eye–nostril and 4/5 internarial distance, 2/3–1/2 the interorbital distance; spiracle sinistral, not tubular, below line connecting eye to root of hind limb, slightly nearer eye than root of hind limb; anus dextral, opening not reaching margin of ventral fin. Mouth ventral, subterminal; beaks black-edged, finely serrate, upper one a smooth arc; papillae small and homogeneous, continuous along lower lip and in 3–4 rows, confined to lateral corners of upper lip; dental formula I: 6–6/1–1: II; very narrow gaps between the two outermost divided rows of upper lip and the divided row of lower lip. Tail 0·54–0·6 of total length, weakly convex, deeper than body at centre, abruptly tapering in last quarter to slender, rather blunt tip; dorsal fin only very slightly deeper than ventral fin and both narrower than caudal muscle at centre. Colour in alcohol of head and body pale greyish brown above, white below, without pattern; tail fins pale grey, caudal muscle yellowish, without pattern.

Range: Peninsular parts of Thailand, W. Malaysia, Nias Is., ? Sumatra.

Rhacophorus reinwardtii (Wagler)

Hypsiboas reinwardtii Wagler 1830 : 200.

MATERIAL: BM 1967.2522–29 (7 ♂, 1 ♀).

HABITAT: On Gunong Benom this species occurs in similar areas and in somewhat similar habitats to *Rhacophorus nigropalmatus* and *R. prominanus*. It is a lowland species and was never seen or heard above 1600 ft yet the G. Benom examples appear to be the first record of the species from Malaya. Specimens were found on the wide logging track in depressions caused by tyre tracks and flooded by rains and in other temporary pools by secondary growth in disturbed forest and near to banana stands, as well as up to 12 ft from the ground on banana fronds, bamboo and bushes that overhung pools.

CALL: *R. reinwardtii* calls from bushes, often bamboo, and from a lower level than *R. nigropalmatus*. Its call is a rat-tat-tat resembling a rattle or a woodpecker's tapping and is softer and quieter than the call of *R. nigropalmatus*.

COLOUR IN LIFE: Dorsum and upper parts of the limbs a soft apple green, sides of body brick red with large, black areas, marbling and spots all of which were outlined with sky blue. Inner surfaces of the arm, of the tibia and to a lesser extent of the tarsus black with pale blue spots. Posterior aspect of thighs grey with very fine black reticulations. Undersurfaces of throat and belly pale yellowish grey or chalky white with black marbling. Iris white. Web between all the toes and all the fingers from base to distal margin intense black with sky blue spots and streaks on both the upper and lower surfaces. Except for the outermost, the fingers and toes were similarly coloured.

REMARKS: While these specimens agree with *reinwardtii* and differ from *bimaculatus* Blgr. in the extent of the web on both fingers and toes, in the tympanic and finger disk sizes and proportions, in head proportions and in the development of dermal appendages (Inger 1966) they exhibit marked differences in size from the Javan and Sumatran populations of *reinwardtii*, and in colour pattern are unlike Javan *reinwardtii* although they show certain resemblances to the var *lateralis* described and figured by Werner (1900) from a single individual obtained at Batu Bahru, Sumatra (Basel Museum 1192). The G. Benom males vary in body length from 59–66 mm (average 63 mm) and the female measures 80·3 mm. Inger (1966) gave a range of 46–55 mm for mature male *reinwardtii* while Wolf (1936) recorded 56 mm for males and 76 mm for females. Five examples of *reinwardtii* obtained in Java and in the British Museum collections have body lengths of 52 mm (3 ♂♂) and 70 and 71 mm for the two females. As can be seen from the description of colour in life, in the G. Benom sample black pigmentation was much more extensive than in Javan populations of *reinwardtii* (Schlegel 1844 plate 30, fig. 4, Van Kampen 1923, fig. 28) and in none of the Malayan examples is the black pigment on the finger and toe web restricted to large black spots between the second and third and third and fourth fingers and between all the toes except the first and second, as occurs in Javan *reinwardtii*.

RANGE: W. Malaysia (Pahang), Sumatra and Java.

SAURIA

Family AGAMIDAE

Aphaniotis fuscus Peters

Otocryptis (*Aphaniotis*) *fusca* Peters 1864 : 385.

MATERIAL: BM 1967.2837–39.

HABITAT: The specimens were found at 700 ft and 2700 ft. No further information on their habitat is available.

RANGE: Peninsular parts of Thailand, W. Malaysia, Borneo, Natuna Is.

Goniocephalus borneensis (Schlegel)

Lophyurus borneensis Schlegel 1848 : 6.

MATERIAL: BM 1967.2840–41 (2 ♂).

HABITAT: The smaller specimen was found on a bush in disturbed forest near Base camp, 700 ft, the larger was caught by a dog near the track in the forest at 1900 ft.

COLOUR IN LIFE: The throat pouch had on each side a vivid pink patch surrounded by bright ultramarine blue. The base of the pouch was yellow green. The trunk was greyish green dorsally with brown edged ocelli on the flanks. Tail black and cream banded.

RANGE: Peninsular parts of Thailand, W. Malaysia, Borneo.

Draco fimbriatus fimbriatus Kuhl

Draco fimbriatus Kuhl 1820 : 101.

MATERIAL: BM 1967.2798–800 (1 ♀, 2 ♂).

HABITAT: The larger of the two males (107·3 mm) was found lying apparently stunned on the verandah of a hut at 700 ft in the forest clearing in early morning. The other male (104·8 mm) was obtained at ca 1900 ft on the ridge southwest of camp 2. The female (101·8 mm) was shot on a tree at 35 ft from the ground in disturbed forest. The tree, 18″ in diameter and at the side of the logging track between Base camp and Kampong Damak at ca 600 ft, had *Draco volans* and *D. punctatus* on it as well, but at a lower height from the forest floor.

COLOUR IN LIFE: The general appearance and colouration of the upper surfaces of this species were of rough bark in shades of grey, black, brown and reddish brown. The wing membranes were indistinctly longitudinally striped black and greyish brown above; their lower surfaces were orange with black spots (♀) or light grey with dark brown spots (♂). In the female the belly, undersurfaces of the base of the tail and of the thighs were orange, the throat pale grey mottled with darker grey and the gular appendage and wattles coral pink. The males had similarly coloured dewlaps and wattles and there were also coral spots on the cheek, chin, and sides of the head. Rather duller orange marks were present on the vertebral region of the large male.

RANGE: Southern provinces of peninsular Thailand, W. Malaysia, Singapore, Gt. Natunas, Sumatra, Java, Borneo.

Draco formosus formosus Boulenger

Draco formosus Boulenger 1900 : 190.

MATERIAL: BM 1967.2801–26 (5 ♀, 19 ♂, 2 juveniles).

HABITAT: The altitudinal range of this species on G. Benom is 700–2500 ft but above camp 2 (1700 ft) it was very rarely seen and only five of the series were obtained from above 1800 ft. All specimens were on trees at heights varying from 8–20 ft from the forest floor. *D. formosus* was more closely associated with the trees skirting the camp clearing and the wide logging tracks than other Dracos and was the commonest species of *Draco* in the area.

COLOUR IN LIFE: Head and body brown above with obscure darker markings. A dark brown transverse band across the upper eyelids and a median dark brown interorbital spot present in both sexes. A pair of jet black spots on the occiput and a pair of more widely separated dark spots farther back on the neck constantly present in the males. Wing membranes mostly yellowish above with five black, somewhat wavy transverse lines, the bands narrower than the interspaces, the distal portion of the wing maroon. Lower wing surfaces similar in colouration but the bands often indistinct. Gular pouch thin and translucent, a whitish grey. Throat and undersurfaces of the wattles blood red. Chin grey with dark reticulations.

REMARKS: The females which contain three or four, usually four, large, broadly oval eggs vary in snout to vent length 74·8–87·6 (average 80·0 mm). Males vary in length from 80·4–102·7 (average 93·7 mm).

RANGE: The nominate form is said to be restricted to S. Thailand and W. Malaysia (Hennig, 1936, Taylor 1963).

Draco maximus maximus Boulenger

Draco maximus Boulenger 1893 : 522.

MATERIAL: BM 1967.2828 (1 ♂).

HABITAT: On tree flanking logging track at ca 800 ft at junction of the track between Base camp and K. Damak and the path leading to camp 2.

RANGE: W. Malaysia, Gt. Natunas, Sumatra, Borneo.

Draco melanopogon Boulenger

Draco melanopogon Boulenger 1887 : 492.

Material: BM 1967.2830–34 (2 ♀, 3 ♂).

Habitat: All specimens were shot in trees among secondary growth flanking the logging tracks and the trail to the stream below Base camp and between 600 and 1000 ft.

Colour in life: Head and vertebral region brown becoming green on the sides of the trunk. Upper surfaces of limbs greenish brown. Some indistinct dark brown cross bars and spots across head and back. Wing membranes black with numerous yellow spots on both upper and lower surfaces. Gular pouch yellowish green in the female, jet black in the male; wattles white in both sexes. Throat, chest and undersurface of forelimbs orange in the male; undersurface of tail similarly coloured.

Remarks: The two females captured 23/24th February are gravid. One measuring 82 mm snout–vent contains only one oviducal egg, 8·0 mm long, the other individual, 79 mm, has the normal *melanopogon* complement of two, each 5·5 mm in length (Inger & Greenberg 1966). The eggs are almost spherical and not distinctly pointed as described by Hendrickson (1966).

Range: Thailand south of the Isthmus of Kra, W. Malaysia, Gt. Natunas, Sumatra, Borneo.

Draco punctatus Boulenger

Draco punctatus Boulenger 1900 : 189.

Material: BM 1967.2828 (1 ♂).

Habitat: The specimen was taken 25–35 ft from the forest floor on a tree near the main logging track at ca 600 ft. In the same tree simultaneously were two other species of *Draco, fimbriatus* and *volans*.

Colour in life: The upper surfaces of the head, body and limbs grey and brown with scattered dark brown speckling. Wings reddish brown above, longitudinally streaked with light grey. Gular pouch pale grey at base, brilliant yellow towards apex, chin yellow spotted grey. Wattles intense lemon yellow. Undersurfaces of the trunk grey-green, of the wings greyish yellow with scattered black spots.

Range: Southern provinces of peninsular Thailand, W. Malaysia, Sarawak.

Draco quinquefasciatus quinquefasciatus Hardwicke & Gray

Draco quinquefasciatus Hardwicke & Gray 1827 : 219.

Material: BM 1967.2829 (1 ♀).

Habitat: Shot on 6″ diameter tree, 10 ft from the forest floor, on the ridge at ca 800 ft NNE of Base camp at noon on 25 February. The individual is gravid and contains four well matured oval eggs, the largest 15·7 mm long.

Colour in life: Ground colour of body yellow-green with broad greyish black cross bands. Wings above orange-red with five broad black cross bands, each with a single row of small white spots confluent with those of the trunk, the orange becoming yellowish medially. Throat green, speckled brown, the wattles black at their bases with a white band, yellowish anteriorly. Gular appendage yellowish orange, belly cream. Undersurfaces of wings yellow becoming orange laterally and posteriorly, with five broad black bands each of which bordered by greyish green, the most posterior band short and not extending to the lateral wing margins.

Range: Extreme southern provinces of peninsular Thailand, W. Malaysia.

Draco volans volans Linnaeus

Draco volans Linnaeus 1758 : 199.

Material: BM 1967.2835–36 (1 ♀, 1 ♂).

Habitat: The female which contains three large (13·4 mm) eggs was seen on the ground in the kitchen quarters of Base camp 700 ft. When disturbed it ran up a low leafy tree and was shot. The male was found 25–35 ft from the forest floor on a tree near the main logging track at ca 600 ft. On the same tree and at the same time *D. f. fimbriatus* occurred but at a greater height, and nearer the ground an example of *D. punctatus* was obtained.

Colour in life: Above, the head, body and wings in both sexes were brown and grey, the grey on the back forming discreet transverse series of spots and lines which extended to the wings. There was a dark brown interorbital spot and in the female a dark medial nuchal spot. The gular pouch in the female was a vivid turquoise blue, in the male brilliant yellow, speckled black at its base. The inner surfaces of the wattles were greyish white. The eyelids in the male were sky blue. The undersurfaces of the trunk and limbs were pale greenish blue medially and yellow-green on the sides (♀) or powder blue (♂). In the female the undersurfaces of the wings were vivid yellow with black interrupted transverse lines and spots, while those of the male were powder blue with black interrupted transverse wavy bands.

Range: Peninsular parts of Thailand, W. Malaysia, Singapore, Sumatra, Java, Borneo, Natunas, Philippines (Palawan).

Family **VARANIDAE**

Varanus bengalensis nebulosus (Gray)

Monitor nebulosus Gray in Cuvier 1831 : 27.

Material: BM 1967.2842 (1 juvenile).

Habitat: The example was found during late afternoon at the entrance to an elliptical hole 18 ft from the forest floor in a tree by the trail, downstream from Base camp, 700 ft.

Range: The subspecies *nebulosus* occurs from S. Burma to S. Vietnam and southwards throughout W. Malaysia and Java.

Varanus salvator salvator (Laurenti)

Stellio salvator Laurenti 1768 : 56.

MATERIAL: BM 1967.2843 (juvenile ♀).

HABITAT: This specimen, which weighed 4 lbs and had a total length of 1450 mm, was obtained from the banks of the stream about ½ mile below Base camp and at about 650 ft. Its stomach contained a mouse deer.

RANGE: The nominate subspecies occurs from Ceylon and India to Thailand, Vietnam and Hainan, W. Malaysia and islands to the south and east as far as northern Australia.

Family **GEKKONIDAE**

Cnemaspis affinis (Stoliczka)

Cyrtodactylus affinis Stoliczka 1870 : 167.

MATERIAL: BM 1967.2781 (1 juvenile).

HABITAT: Camp 2 clearing, 1700 ft.

RANGE: Southernmost provinces of Thailand, W. Malaysia.

Cnemaspis kendallii (Gray)

Heteronota kendallii Gray 1845 : 174.

MATERIAL: BM 1967.2782 (1 ♀).

HABITAT: On kitchen table at Base camp during afternoon, 700 ft.

RANGE: Thailand, W. Malaysia, Singapore, Gt. Natuna Is., Borneo.

Cyrtodactylus ?brevipalmatus (Smith)

Gymnodactylus brevipalmatus Smith 1923 : 48.

MATERIAL: BM 1967.2783 (1 ♂).

HABITAT: At night on leaf litter of forest floor near Base camp clearing and stream at 700 ft.

REMARKS: The G. Benom example differs from the holotype, from a juvenile also obtained in Nakhon Si Thammarat and from a female collected in Raheng, N. Thailand 2500 ft, in having fewer trunk tubercles and in their being disposed in approximately three longitudinal paravertebral rows that do not extend to the flanks. It further differs from the type in lacking femoral pores and in having only eight preanal pores. The tail is not cylindrical but is noticeably depressed and has almost vertical sides so that in section it is squarish. Tail denticulation appears to be less pronounced in the type but this may be artifact and due to preservation although the pointed tubercles along the dorsolateral edges are certainly shorter than in the G. Benom example. The toe web, the number of ventral scales at midbody between the lateral folds (44) and the number of the digital lamellae agree with the type and the other examples, but dilation of the basal phalanges appears to be greater. Smith's figure of the toes of *brevipalmatus* (1923, pl. 5) is inaccurate in omitting the plates under the distal portion of the distal halves.

RANGE: Known only from specimens obtained in the Nakhon Si Thammarat Mts., Peninsular Thailand, from Raheng, N. Thailand (Smith 1935), and from the Gunong Benom individual.

Cyrtodactylus consobrinus (Peters)

Gymnodactylus consobrinus Peters 1871 : 569.

MATERIAL: BM 1967.2784 (1 juvenile).

HABITAT: The specimen was smoked out of a hole in a live tree in the valley below camp 2, at about 1600 ft.

RANGE: W. Malaysia and Borneo.

Cyrtodactylus marmoratus (Kuhl)

Phyllurus marmoratus Kuhl in Fitzinger 1826 : 47.

MATERIAL: BM 1967.2785–95 (6 ♀, 4 ♂).

HABITAT: The series was obtained in forest between 700 and 3500 ft. Most examples were found at night on branches and trunks of trees, one being on the undersurface of a large, rotten tree trunk that had fallen across the boulder strewn stream bed in the valley below camp 3, another inhabited a hole between the roots of a 6″ diameter tree close to the camp 3 huts and emerged from its hole soon after dusk to crawl up the trunk. At the lower elevations a few individuals were found on the high bank at the side of the logging track.

REMARKS: These specimens agree well with all the diagnostic characters of *marmoratus* except for the position and number of pores in the males. The male *C. marmoratus* is said to be characterized by both preanal and femoral pores and a longitudinal preanal groove, the preanal pores numbering 12 or 13, the femoral pores 4–6 on each side (Boulenger 1912) but while these G. Benom specimens have a row of enlarged femoral scales none of the scales has a pit or pore and there are, at the most, only five preanal pores in a V-shaped line. They vary in body size from 55·4–61·3 mm.

RANGE: Thailand, W. Malaysia, Sumatra, Java, Borneo, Celebes, New Guinea, Christmas Island.

Gehyra mutilatus (Wiegmann)

Hemidactylus mutilatus Wiegmann in Meyen 1835 : 238.

MATERIAL: BM 1967.2796–97 (1 ♀, 1 ♂).

HABITAT: Both specimens were smoked out of live trees in the forest near camp 2 at 1700 ft.

RANGE: Widely distributed from Ceylon and S. Burma to S. China, Japan, Thailand, W. Malaysia, Indo-Australian Archipelago, Oceania and islands in the Indian Ocean.

Family **SCINCIDAE**

Lygosoma (Scincella) vittigerum vittigerum Boulenger

Lygosoma vittigerum Boulenger 1894 : 615.

MATERIAL: BM 1967.2854 (1 juvenile).

HABITAT: The specimen, which has a body length of only 17·5 mm, was found during the morning on the bark of a tree close to camp 2 at 1700 ft.

RANGE: Peninsular parts of Burma and Thailand, W. Malaysia, Sumatra, Mentawei Is., Borneo.

Mabuya multifasciata (Kuhl)

Scincus multifasciatus Kuhl 1820 : 126.

MATERIAL: BM 1967.2844–53 (4 adults, 6 juveniles).

HABITAT: This species was the most common lizard in and around camp at 700 ft, invariably frequenting secondary growth. Individuals were obtained from the ground, on and among fallen leaves, on piles of felled branches, on a pile of sand at the edge of the track, as well as apparently asleep on the trunk of a tree.

COLOUR IN LIFE: Taylor's description (1963) of the colour pattern of this species applies equally well to the G. Benom examples but on the chin, throat and chest of one adult male was mustard yellow, the rest of the ventral surfaces being a greyish green. From the tympanum to the flanks this individual was a reddish orange. The lateral ocelli may or may not be clearly marked and the dark brown lateral stripe may or may not be bordered above by a light, longitudinal dorsolateral stripe 1½ scales wide.

REMARKS: The midbody count in these examples is 34(7) and 32(3). The first loreal is usually lower than the second, rarely of similar height. In each specimen the frontonasal forms a suture with the nasal and generally a broad suture. Both the head shields and the dorsal trunk scales have dark streaks at their edges, usually at the posterior borders of the head shields and at the lateral edges of the body scales.

Range: From N.E. India to S. China, Thailand, W. Malaysia, Singapore, Sumatra, Java, northwards to the Philippines and eastwards to New Guinea.

Sphenomorphus indicus indicus (Gray)

Hinulia indica Gray 1853 : 388.

Material: BM 1967.2855 (1 juvenile).

Habitat: On fallen tree trunk and among dead leaves on peaty ground at 3650 ft during the afternoon.

Remarks: This individual, and two juveniles obtained at Bukit Fraser which were reported on by Smith (1922b & 1930), differ somewhat from the nominate form of *indicus*. They have a higher midbody count (36) than in both Tennasserim examples (30–32: 32 in the types of *zebratum*) and the average N.W. Thailand specimen (34·3: N 17) (Taylor 1963) and the number of subdigital lamellae on the fourth toe is slightly greater (22–24) than in the adult *zebratum* syntype, in N.W. Thailand examples (18–19) and in the *indicus* types (19 : 20, 18 : 20). Both Smith (1935a) and Taylor (1963) err in stating that the frontal is as long as—or longer (Smith)—than the combined parietals for while this is so in the syntypes of *indicus* and in the adult *zebratum* syntype, in the juvenile *zebratum* syntype and in both the Gunong and Bukit Fraser examples the frontal is 3/4 the distance from its posterior border to the posterior border of the parietals, measured along the midline.

Range: From India to central China and southwards to W. Malaysia.

SERPENTES

Family **TYPHLOPIDAE**

Typhlops diardi mulleri Schlegel

Typhlops Mülleri Schlegel 1839 : 32.

Material: BM 1967.2267.

Habitat: Among leaf litter at base of tree in Base camp clearing, 700 ft.

Range: Tenasserim through Thailand to S. Vietnam, also W. Malaysia, Singapore, Sumatra and Borneo.

Family **NATRICIDAE**

Natrix trianguligera (Boie)

Tropidonotus trianguligerus Boie 1827 : 535.

Material: BM 1967.2273 (1 ♀).

Remarks: The specimen was found at night swimming in a still backwater of the stream at Base camp, 700 ft. In life the sides of the anterior half of the trunk were brick red, the upper surface of the head dark olive, the iris light olive. Upper labials and mental pale buff-coloured, venter pale yellowish.

Scale rows	19
Ventrals	139 + 2
Sub caudals	93

RANGE: Peninsular parts of Burma and Thailand, S. Vietnam, W. Malaysia, Singapore, Sumatra, Java, Mentawei Is., Borneo, Celebes.

Amphiesma sarawacensis (Günther)

Tropidonotus sarawacensis Günther 1872 : 596.

MATERIAL: BM 1967.2274–5 (2 ♂).

REMARKS: The two specimens appeared within five minutes of each other on the soft peaty soil behind the log fire in camp 4 (5000 ft) at 1300 hrs. Their colouration was as described by Tweedie (1954) for this species.

	2274	2275
Scale rows	17	17
Ventrals	139 + 2	140 + 2
Subcaudals	77	32 +

The gall bladder is situated deep to ventral 50.

RANGE: W. Malaysia, Borneo.

Macropisthodon rhodomelas (Boie)

Tropidonotus rhodomelas Boie 1827 : 535.

MATERIAL: BM 1967.2282 (1 ♂).

REMARKS: Found midmorning on the ground among forest litter at the timber stack at junction between main path from Base camp and track to camp 2.

Scale rows	19
Ventrals	132 + 2
Subcaudals	54

RANGE: Peninsular Thailand, W. Malaysia, Singapore, Sumatra, Java, Borneo.

Family **COLUBRIDAE**

Elaphe flavolineata (Schlegel)

Coluber flavolineata Schlegel 1837 : 141.

MATERIAL: BM 1967.2287 (1 ♀).

HABITAT: On track above camp 2 at approximately 1800 ft.

COLOUR IN LIFE: Body green above, the dorsal scales edged with black, with indistinct yellowish transverse bands on the mid body that became orange farther back and more clearly defined. Ventrals yellow and narrowly edged with black, underside of tail with broad orange bands, 6–7 scales in length on a greenish ground. Upper labials vivid yellow. A black temporal blotch.

Scale rows	19
Ventrals	236
Subcaudals	116 + (tip of tail missing)
Upper labials	9 5th and 6th entering eye
Temporals	2 + 2

RANGE: Andamans, Peninsular Burma and Thailand, W. Malaysia, Singapore, Sumatra, Java, Mentawei Is., Borneo, Celebes.

Gonyophis margaritatus (Peters)

Gonyosoma margaritatum Peters 1871 : 578.

MATERIAL: BM 1967.2278 (1 ♂).

REMARKS: This specimen was found at about 2750 ft crossing the track between camps 2 and 3. In life it was most beautifully coloured, the upper parts being pale green with the dorsals heavily margined in black and with yellowish, broad cross bands on the posterior two-thirds of the body and tail that became brick red towards the tail. On the undersurfaces of the snake the mental and first and second labials and sides of the snout were orange, the rest of the labials and the throat yellow, the ventrals as far as V34 were also yellow and farther back an orange midventral line developed that became deep orange with blackish cross bars. There was a deep black temporal band.

Scale rows	19
Ventrals	238 + 2
Subcaudals	128
Total length	570 mm

RANGE: W. Malaysia (Perak, Pahang, Kelantan), Borneo.

Liopeltis longicauda (Peters)

Ablabes longicaudus Peters 1871 : 574.

MATERIAL: BM 1967.2268–70 (2 ♂, 1 ♀).

REMARKS: 750 ft. Two of the specimens were found in coitus on the main track leading from Base camp at midday on 21st February. The third specimen was obtained in the same area. All three differ from Tweedie's description (1957) of the species in having the venter from the throat to the tail tip yellow. The chin was white in life and the head and nape markings white.

	2268	2269	2270
Sex	♂	♀	♂
Scale rows	13	13	13
Ventrals	116	114	116
Subcaudals	12 +	24 + 1	54 + (tail damaged)

The gall bladder is situated deep to ventral 74 in the male and deep to ventral 79 in the female.

Liopeltis baliodeirus (Boie)

Coronella baliodeira Boie 1827 : 539.

Material: BM 1967.2271 (1 ♂).

Remarks: Found during late afternoon at about 1000 ft on the track between Base camp and camp 2. The undersurfaces of the posterior half of the body and all of the tail were orange in life.

Scale rows	13
Ventrals	121 + 2
Subcaudals	72

Range: Peninsular Thailand, W. Malaysia, Singapore, Sumatra, Java, Natuna Is., Borneo.

Pseudorhabdion longiceps (Cantor)

Calamaria longiceps Cantor 1847 : 63.

Material: BM 1967.2272 (1 ♀).

Remarks: 700 ft. The specimen was dug out of a rotting hollow log in the forest near Base camp. In life the head was a dull blood red, the collar yellowish and the trunk dark brownish red.

Scale rows	15
Ventrals	135
Subcaudals	29

Range: Southernmost provinces of Thailand, W. Malaysia, Singapore, Sumatra, Borneo, Celebes and ? Philippines (Taylor 1965).

Family **DIPSADIDAE**

Calamaria lumbricoidea Boie

Calamaria lumbricoidea Boie 1827 : 540.

Material: BM 1967.2279 (1 ♂).

Remarks: The individual was found at 21 00 hrs. crossing the earth floor of the kitchen at Base camp (700 ft). The dorsum except for the upper labials is brown and without stripes and most of the body scales have a darker brown apical spot. The lips are cream. The venter has black bars, each bar covering two adjacent ventral scales and separated from the next by a varying number of yellowish scales but usually by 3, 4 or 5. The absence of stripes in this specimen, coupled with a ventral count of 172 and four gulars between the posterior chin shields and the first ventral, agree better with individuals obtained from states on the western side of the peninsula than with Pahang *lumbricoidea* (Inger 1965).

The hemipenis is forked and papillate.

Scale rows	13
Ventrals	172 + 1
Subcaudals	24
Supralabials	6 (3–4)
Temporals	0 + 1

RANGE: Southern Thailand to Java, Borneo and Leyte (Inger 1965).

Lepturophis borneensis Boulenger

Lepturophis borneensis Boulenger 1900 : 183.

MATERIAL: BM 1967.2294 (1 ♂).

REMARKS: The G. Benom individual appears to constitute the first record of the occurrence of *Lepturophis* in the Malayan Peninsula. Previously this monotypic genus was known only from the type obtained in Sarawak and from a subsequent series of twelve in the Field Museum Chicago, from Sabah and Sarawak.

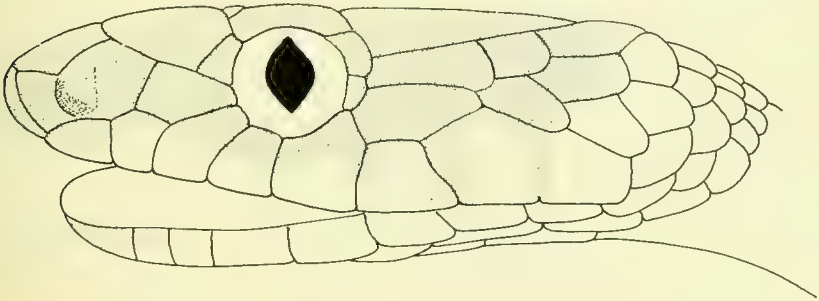


FIG. 2. *Lepturophis borneensis* (B.M. 1967.2294).

Boulenger (1900a) likened the teeth of *Lepturophis* to those of *Lycodon* and gave the formula of the type specimen as 6 + 6. The type specimen has not been examined by me; it is probably in the Kuching museum, Sarawak, but confirmation has not been received. The G. Benom example has been compared with the Field Museum series assigned to *Lepturophis* which in scale counts and in dentition agree favourably with the G. Benom specimen. See table A, p. 47. The only resemblance between the teeth of *Lycodon* and those specimens examined here is in the large fang-like anterior maxillary tooth followed by a diastema then a series of small teeth. In the G. Benom individual the maxillary formula is 6 + 6 + 3, the first six gradually increasing in size, the second group of six being small and of more or less equal size while the posterior group are again fang-like. The left maxilla of FMNH 158650 which was dissected out appears to have a formula of 6 + 3 + 3 but FMNH 148895–6 have series of six small teeth in the centre of the maxillae. These enlarged rear teeth are of a curious shape; their medial surfaces are flat but on the lateral surfaces flattening is restricted to the anterior and posterior surfaces of the teeth with the central portion of each tooth rounded externally and thus semicircular in transverse section. The flat flanges on the posterior and anterior borders of the tapering teeth give them sharp, cutting edges. Similar lateral compression of the anterior and posterior surfaces of the maxillary teeth occurs in *Xenopeltis* (Thomson 1913) but in that genus the teeth have blunt tips and a blade-like appearance and moreover are set at an oblique angle to the long axis of the jaw. Lateral compression of the teeth is also developed in *Iguanognathus* which however has spatulate, chisel-shaped teeth with broad tips and of quite a different type. The notched and grooved ventrals, coupled with the extremely slender, elongate body (total length of G. Benom example 167·6 cms) suggest that *Lepturophis* is an arboreal snake, although the Malayan example was found on the ground at night on the main track near Base camp at 700 ft and the Field Museum series was collected in or on the banks of forest streams.

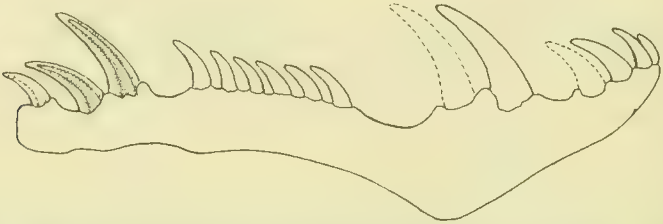


FIG. 3. Maxilla and maxillary teeth of *Lepturophis borneensis* (B.M. 1967.2294).

In life the snake was a uniform dark grey dorsally with a whitish venter.

RANGE: W. Malaysia (Pahang), Borneo (Sabah, Sarawak).

Macrocalamus jasoni sp. nov.

HOLOTYPE: BM 1967.2283, a gravid female from leaf litter on track below camp 5 at about 5800 ft, Gunong Benom, C. Pahang, W. Malaysia, collected by John A. Bullock, April 9th 1967.

PARATYPES: BM 1967.2284, female, from leaf litter on forest floor of summit knoll above camp 5 Gunong Benom, 6500 ft collected by Lord Medway, March 27th 1967. BM 1967.2285, female, locality as holotype collected by Bah Chung, April 9th 1967.

DESCRIPTION OF HOLOTYPE: Midbody scales in 15 rows, ventrals 131, subcaudals 17. Loreal precisely twice as long as deep, one preocular, one postocular, 1 + 2 temporals, 8 upper and 7 lower labials, the fourth and fifth upper labials entering the eye, the fourth making contact with the loreal. Gall bladder deep to ventral 96, maxillary teeth 11, palatine teeth 11, pterygoid teeth 19. The colour in life was iridescent black on the dorsum with a conspicuous pair of dorsolateral yellow ochre

TABLE A

Scale counts in *Lepturophis borneensis*

Museum No.	Locality	Sex	D	V	C	Upper labials	Lower labials	Postocular	Preocular	Temporals
TYPE	Sarawak	?	17	241 + 2	193	8 (3–5)	(5)	2	1	2 + 2
FMNH 63597	Sabah: Sandakan Dist.	♀	17	238 + 2	179 + S	$8\,\frac{(3\text{–}5)\S}{(3\text{–}6)}$	9 (5)	2	1	2 + 2 + 2
63598		♀	17	227 + 2	182 + S	8 (3–5)	9 (5)	2	1	$\frac{2 + 2 + 3\Vert}{2 + 2}$ or $\frac{2 + 2}{2 + 2}$
138667	Sarawak 3rd Div.	♀	17	230 + 2	113 +	8 (3–5)	9 (5)	2	1	2 + 2 + 2
145709	,, ,,	♂	17	244 + 2	189 + S	9 (3–5)†	9 (5)	2	1	2 + 2 + 2
148893	,, ,,	♀	17	225 + 2	170 + S	8 (3–5)	9 (5)	2	1	2 + 2 + 2
148894	,, ,,	♀	17	230 + 2	174 + S	8 (3–5)	9 (5)	2	1	2 + 2 + 2
148895	,, 4th Div.	♀	17	228 + 2	167‡	8 (3–5)	9 (5)	2	1	2 + 2 + 2
148896	,, ,,	♂	17	243 + 2	203 + S	8 (3–5)	9 (5)	2	1	2 + 2 + 3
148897	,, ,,	♀	17	230 + 2	171 + S	8 (3–5)	9 (5)	2	1	2 + 2 + 3
158649	,, ,,	♂	17	243 + 2	206 + S	8 (3–5)	9 (5)	2	1	$\frac{2 + 2 + 3}{2 + 2 + 2}$
158650	,, ,,	♀	17	229 + 2	176 + S	8 (3–5)	9 (5)	2	1	2 + 2 + 2
158651	,, ,,	♀	17	231 + 2	175 + S	8 (3–5)	$\frac{9\ (5)^{*}}{8\ (4)}$	2	1	2 + 2 + 2
BM 1967.2294	G. Benom	♂	17	247 + 2	185 + ¶	8 (3–5)	9 (5)	2	1+ loreal	2 + 2 + 3

* Left side 3 & 4 fused.
† On both sides another "upper labial" between the 2nd and 3rd is excluded from the mouth.
‡ About 5 or 6 missing.
§ Dorsal origin of suture between 5th and 6th left upper labials obscured by scratches.
‖ Third right upper temporal may be caused by a break in the 2nd upper temporal.
¶ About 7 missing.

stripes which extend from the temporals to the tip of the tail. These stripes which are two scales wide and are separated from each other by three scales are bordered below by black, the black extending from the fourth longitudinal dorsal row of scales to the lateral fifths of the ventral scales. The ventrals, apart from their black lateral margins and medial black flecks on ventrals 1–8 are bright yellow. The subcaudals are yellow except for occasional black speckling at their medial margins.

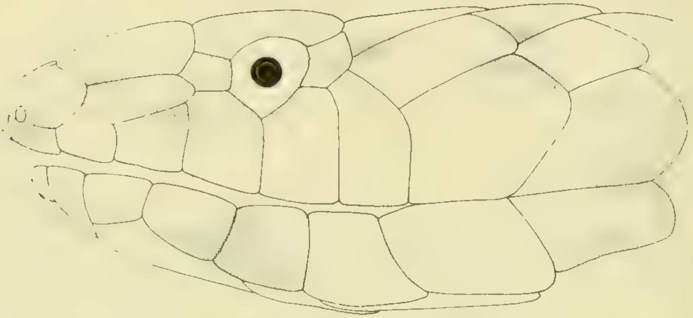


FIG. 4. *Macrocalamus jasoni* Holotype.

The head is brownish yellow with blackish areas on the prefrontals, loreal, pre- and postoculars, anterior temporal and labials, except for the sixth upper labial which is entirely yellow. From the last upper labial to the last lower labial the black colouration forms a broad but rather ill-defined vertical bar. The mental and first lower labials are black and the black extends on to the anterior chin shields where it surrounds a yellowish oval patch on each shield.

Total length 760 mm, midbody girth 237 mm.

VARIATION: The paratypes are similar to the holotype in dorsal colouration and in their stocky build but are considerably smaller in total length (380 mm and 550 mm). Apart from black tips to the outer margins of the ventral scales the undersurfaces of 2285 are a uniform yellow but in 2284 most ventral and subcaudal scales have a medial black patch or streak in addition to the lateral black marks In the paratypes the ventral and subcaudal counts are 132, 134 and 22, 20, and the arrangement of the head shields corresponds closely with that of the holotype. The gall bladder was situated deep to ventral 96 in BM 1967.2285 and V88 in BM 1967.2284.

RELATIONSHIPS AND ECOLOGY: In its pattern and in its considerably larger size and much more robust proportions *M. jasoni* differs strikingly from the two other species of *Macrocalamus* that are known. It is further distinguished from *M. lateralis* Günther by its higher number of pterygoid teeth and from *M. tweediei* Lim by its lower ventral count. Neither *lateralis* nor *tweediei* has dorsolateral stripes, *lateralis* commonly being a uniform reddish brown above but occasionally having light chevrons on the head and nape while *tweediei*, known only from the holotype and paratype, is said to be uniform black above with a black and yellow chequered venter (Lim 1963). None of the *jasoni* specimens has the thin pale longitudinal line along the lowermost row of dorsal scales that is formed from a whitish spot on each scale and is characteristic of *M. lateralis*, nor the bright coral red venter of *M. lateralis* (Boulenger 1912). But the most remarkable distinguishing feature of *jasoni* is its size and bulk at sexual maturity which are at least twice those of either *lateralis* or *tweediei*. Gravid female *lateralis* vary in body length from 220 to 280 mm, whereas the gravid holotype of *jasoni* measures 700 mm from snout to vent. The female paratype of *tweediei*, FMNH 109868, which according to Inger (pers. comm.) seems to be sexually mature is stated by Lim to be 348 mm, but this measurement may include the broken tail.

No differences in external meristic characters could be found between *M. jasoni* and *M. lateralis* although the ventral count of *jasoni* (131–134) is in the upper part of the wide range of variation noted in female *lateralis* (116–136, N 16).

Dental counts which were made on a number of British Museum and University of Malaya examples of *M. lateralis*, on the paratype of *M. tweediei* and on the three *M. jasoni* were found to be of value in demonstrating further differences between the three taxa. While the number of maxillary and palatine teeth in *jasoni* (M 11–13, P11) fall within the range of the counts for ten examples of *lateralis* (M 10–14, P9–12) the number of pterygoid teeth is non-overlapping. *M. jasoni* has 19, 20 and 21 in the three type specimens while 10 examples of *lateralis* from which pterygoids were dissected out varied from 13–18 (mean 16) teeth, only the type having 18. Dr Inger, who kindly examined the paratype of *tweediei* reports that the right maxilla has 18 teeth (subequal), right palatine has 13 and the right pterygoid 23. In each of these dental counts *tweediei* is outside of the range of both *lateralis* and *jasoni*. An interesting comparison can be made by analysing these figures by the provenance of the individuals. The pterygoids of seven *lateralis* obtained in the Larut Hills and Maxwell Hill vary from 14–16 while those lacking a locality have 16, 17 and 18, the highest count being in the type. The number of maxillary teeth in the type are also higher (14) than in the other *lateralis* that were examined (10–12) and this raises some doubt about the origin of the type specimen and of whether dental counts in *Macrocalamus* may vary geographically. No precise locality is available for the type of *lateralis* but Lim (1963) restricts it to Cameron Highlands. The series of *lateralis* collected on the Cameron Highlands (Lim 1963 & 1967) has not been seen by me but I would venture to suggest that an examination of their pterygoid teeth and a comparison of counts with those made on Larut Hills material would reveal whether or not dental formulae in *Macrocalamus* are subject to geographical variation, and if they are, whether the restriction of the type locality of *lateralis* to Cameron Highlands is appropriate. The higher number of pterygoid teeth in *jasoni* presumably has some dietary significance although there is no evidence of *jasoni* having different feeding habits from *lateralis*. The stomach of the holotype of *jasoni* is empty.

All three species of *Macrocalamus* occupy similar ecological niches. The *jasoni* series were obtained in a damp habitat among leaf litter or crossing the track. Lim (1963) records *lateralis* and *tweediei* from under logs in a damp environment at 6000 ft on G. Bringchang. The highest altitude from which *M. lateralis* has been obtained is 6300 ft (Lim 1967). All other published records of the vertical distribution of this species indicate that it occurs between 3500 and 5700 ft (Boulenger 1912, Flower 1899, Smith 1922) in the Larut and Maxwell Hills, Perak, Cameron Highlands and G. Tahan, Pahang. *M. tweediei* has so far been found only on G. Brinchang, Cameron Highlands, at 5000 and 6000 ft (Lim 1963) where at the higher elevation it was in close association with *M. lateralis.* Lim (1967) described *lateralis* as being (with *Pareas vertebralis*) the commonest snakes on Gunong Brinchang and often found on the road basking in the early morning sun. Both Tweedie (1954) and Lim (1967) stated that *lateralis* eats insects and their larvae.

The specific name is appropriate in view of the striking golden ventral markings of the species; it is also cordially dedicated to the Hon. J. Jason Gathorne-Hardy, son of Lord and Lady Medway.

Pareas vertebralis (Boulenger)

Amblycephalus vertebralis Boulenger 1900 : 307.

MATERIAL: BM 1967.2277 (1 ♀).

REMARKS: This snake was found at night on a branch of a tree about 200 yards from camp 4 (5000 ft) on the trail leading to the water hole. The snake's eyes reflected a bright red in torchlight.

Scale rows	15
Ventrals	202 + 1
Subcaudals	66
Supralabials	7 (3–5)
Loreal	1
Postoculars	1
Temporals	2 + 2

RANGE: W. Malaysia (mountains of Perak and Pahang).

Pareas malaccanus (Peters)

Asthenodipsas malaccana Peters 1864 : 273.

MATERIAL: BM 1967.2276 (1 ♀).

REMARKS: Collected on the high bank at the side of the main track from Base camp, at about 800 ft. Ground colour black with irregular brownish grey cross bands bordered with white. Head silvery white.

Scale rows	15
Ventrals	158 + 1
Subcaudals	37

RANGE: S. Thailand (Yala Prov.), W. Malaysia, Sumatra, Borneo (Taylor 1965).

Family **ELAPIDAE**

Maticora intestinalis (Laurenti)

Aspis intestinalis Laurenti 1768 : 106.

MATERIAL: BM 1967.2280–81 (2 ♀).

REMARKS: Both examples were found at night on steep slopes between 2000 and 3500 ft. When disturbed, the snake made no attempt to raise its tail and expose the vivid red undersurface, contrary to the normal behaviour of this species. In life the vertebral line from behind the frontal to the tail tip was red. Flanking the line were dark brown longitudinal bands which below were edged with a white line. The undersurface of the body had broad black and white bands of equal width.

	2280	2281
Scale rows	13	13
Ventrals	239 + 1	244 + 1
Subcaudals	26	24
Supralabials . . .	6 (3–4)	6 (3–4)
Preoculars	1	1
Postoculars	2	2
Temporals	1 + 2	1 + 2

RANGE: Thailand, W. Malaysia, Singapore, Java, Borneo.

Bungarus flaviceps (Reinhardt)

Bungarus flaviceps Reinhardt 1843 : 267.

MATERIAL: BM 1967.2286 (1 juvenile).

REMARKS: This specimen was found in an area between the disturbed forest around Base camp and the plantations near K. Damak. It is in poor condition.

RANGE: Peninsular Burma, Thailand, S. Vietnam, W. Malaysia, Sumatra, Java, Borneo.

Trimeresurus hageni (Lidth de Jeude)

Bothrops hageni Lidth de Jeude 1886 : 54.

MATERIAL: BM 1967.2290–91 (1 ♂, 1 ♀).

HABITAT: One of the individuals (2291) was found in the late afternoon among ferns four to five inches from the forest floor by a narrow stream in the valley below camp 2, at about 1600 ft. The other example was obtained in the area of Base camp at approximately 700 ft.

REMARKS: Brongersma (1933) distinguished *hageni* from *sumatranus* on the basis of colour pattern, the number of upper labials in contact with the subocular and the juxtaposition of the supranasals. Both of the G. Benom individuals have the *hageni* pattern, that is the trunk scales are narrowly edged with black but have no black crossbands, and a light lateral line along the first and second rows of dorsals and bordered below by a series of dark spots is present. A light streak (pink in life) from behind the eye to above the last supralabial is also present. Along the sides of the body from the neck to the vent is a series of light spots which in life are pinkish in colour. The spots continue on to the proximal half of the tail where they coalesce to form pinkish crossbands. The distal half of the tail is entirely pinkish in life. In head squamation however the two specimens differ, one agrees with Brongersma's diagnosis of *hageni* in having contiguous supranasals and in two of the upper labials, the third and fourth, making contact with the subocular while the other (2290) has a small scale separating the supranasals and none of the upper labials is in contact with the subocular. The ventral and subcaudal counts for the female are 181 and 74, for the male 182 and 85.

In the British Museum collections are two additional specimens that Dr A. R. Hoge has referred to *T. hageni*. One obtained by Malcolm Smith at Kuala Teku, Pahang (BM 1936.9.12.5) is a ♂ and has 185 ventrals and 79 subcaudals. Its supranasals are in contact and on the right side of the head the third upper labial meets the subocular and on the left side the third and fourth. Its pattern closely resembles that of the G. Benom individuals. The other specimen identified as *hageni* (BM 80.9.10.7), an adult ♀, was collected in Singapore. Its counts are V185 C69 and it not only lacks the spots of the other examples but has indistinct black crossbanding on the trunk. Its supranasals are separated by a large internasal and the third supralabial (LHS) or the third and fourth (RHS) make contact with the subocular.

RANGE: I believe these specimens constitute the first published record of the occurrence of *T. hageni* in Malaya. Brongersma (1933) examined examples of the species from Sumatra, Banka, Simalur, Batu Is., Nias and Mentawei Is.

Trimeresurus popeorum Smith

Trimeresurus popeorum Smith 1937 : 730.

MATERIAL: BM 1967.2289 (1 ♀).

HABITAT: Found during the day lying motionless at the side of the narrow trail above camp 3 at about 3700 ft.

COLOUR IN LIFE: Upper surface of body uniform green, venter paler green. Tail wine red, green below.

Ventral 165
Subcaudals 62
Body length 680 mm
Tail length 133·8 mm

RANGE: E. Himalayas to Cambodia, W. Malaysia, Sumatra and Borneo.

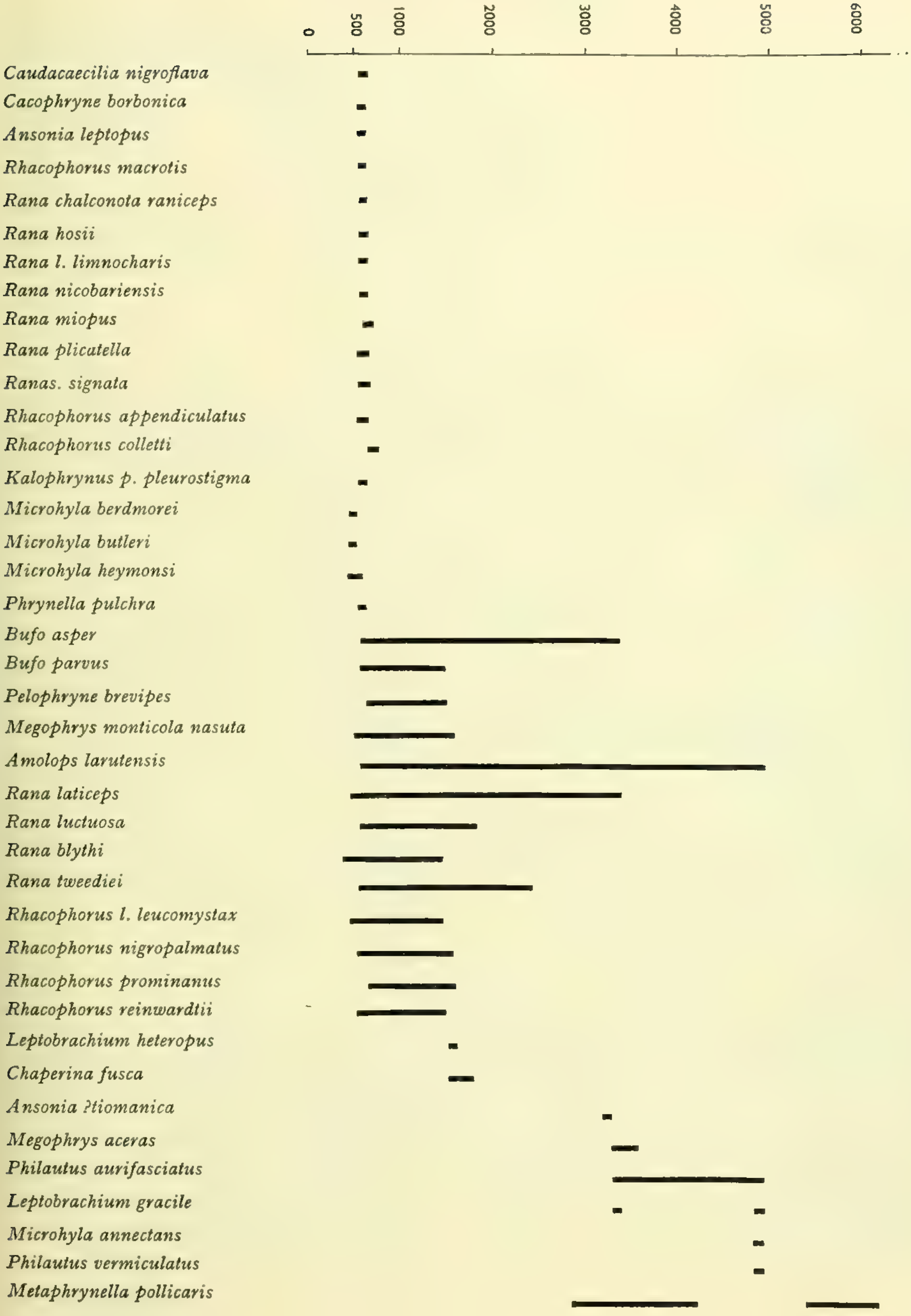
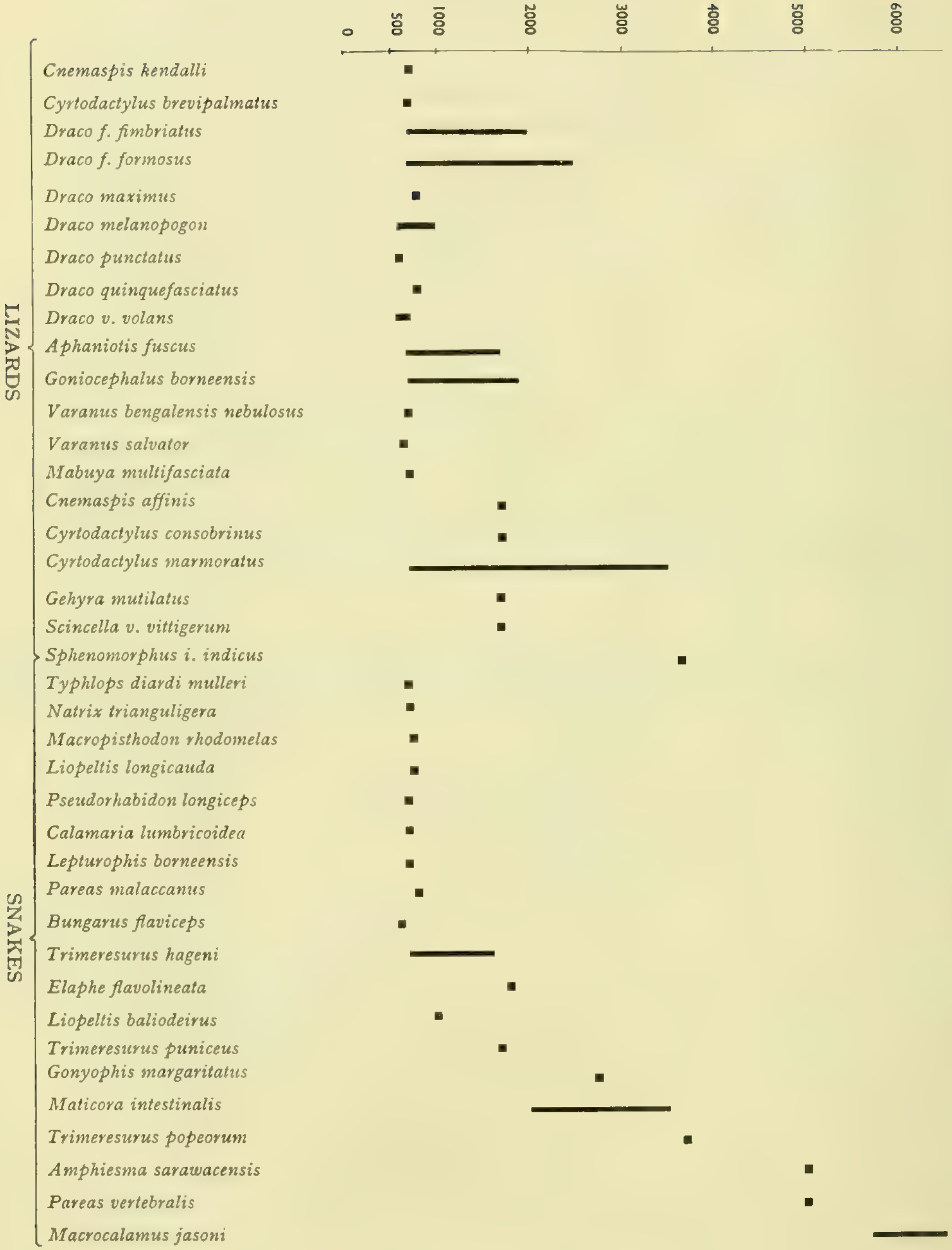


TABLE I

Altitudinal distribution of Gunong Benom amphibians

Altitude in feet



Altitudinal distribution of Gunong Benom reptiles

Trimeresurus puniceus (Boie)

Cophias punicea Boie 1827 : 561.

MATERIAL: BM 1967.2292–3 (1 ♀, 1 ♂).

HABITAT: One specimen was found on a tree at 1700 ft, the other on a fallen tree between Base camp and camp 2.

Ventrals 162 (♂), 158 (♀)
Subcaudals 54 (♂), 49 (♀)

RANGE: Peninsular Thailand, W. Malaysia, Sumatra, Mentawei Is., Java, Natuna Is., Borneo.

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Tribute must be paid to the other members of the herpetology team, Félice V. Slade, Ben Ensol and Inche Sipang. Without Félice Slade's enthusiasm, energy and keen eyesight the results of the team's field work would undoubtedly have been very much poorer. The sagacious Ben Ensol guarded and guided 'the ladies' and provided not only much material but innumerable aids to camp comfort. The unobtrusive, conscientious Inche Sipang also made notable contributions in his own inimitable way.

Members of the other teams and especially the porters, in particular the industrious Kam Mee Chow and the agile Berim bin Uda, also helped enormously both by collecting as time and opportunity allowed and by making expedition life so much more pleasant and profitable.

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THE GUNONG BENOM EXPEDITION 1967

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BY

LORD MEDWAY
School of Biological Sciences
University of Malaya

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THE GUNONG BENOM EXPEDITION 1967

6. THE DISTRIBUTION AND ALTITUDINAL ZONATION OF BIRDS AND MAMMALS ON GUNONG BENOM

By LORD MEDWAY

SYNOPSIS

During 2½ months February to mid-April in 1967, and three weeks in February 1968, birds and mammals were collected and observed on the north-east flank of Gunong Benom from 600 ft to the summit at 6916 ft. Evidence from specimens autopsied confirms that these dates covered the start of the annual breeding season of birds, and was also a period when many mammals were pregnant or lactating. Totals of 191 species of birds and 81 species of mammals were identified. The greatest faunal diversity among both classes was recorded at lower altitudes, with a significant proportion of species present only below 1000 ft. With increasing altitude there was a regular decline in diversity, and only 31 bird species and 10 mammal species were recorded at 6000 ft and above. In both classes, the highland community above 4000 ft was distinct from the lowland community occurring below 2000 ft. The difference was most marked in birds, among which only one species, a cuckoo-dove, was found at all elevations. Among birds, also, at least six species showed a restricted distribution in middle altitudes, and among mammals one species, a bat, was found only at 6000 ft. Subjective assessments of faunal zonation are supported by calculations of Soerensen's coefficient for faunal communities of arbitrary zones separated by '000 ft contours. Bird-netting results are also analysed using a rank-correlation technique, which supports other findings, while emphasizing the distinctiveness of the sub-canopy fauna susceptible to capture by netting.

INTRODUCTION

The bird and mammal faunas of Malaya are adequately known, and the distributions, including altitudinal limits, of most common species are recorded in publications including Robinson (1928), Gibson-Hill (1949) and Glenister (1952) for birds, and Chasen (1940), Harrison (1964) and Medway (1969) for mammals. Collection and observation, however, have been uneven. A disproportionate number of highland records have been made in the hill-station resorts (notably Cameron Highlands and Fraser's Hill), where settlement has opened up the country and undoubtedly affected the local ecology. Few observations have been made in the lowlands adjacent to these montane areas, and the intervening hillsides and the submontane zone have been poorly investigated.

The expedition to Gunong Benom thus offered an unprecedented opportunity to sample the birds and mammals of undisturbed forest on a continuous transect ascending one flank of a mountain which is among the highest in Malaya. The distance in plan from Base camp at 700 ft to the summit at 6916 ft is only 7 miles. The geology of the transect is uniform (Medway, 1972), and the vegetation is consequently determined by altitude and aspect, not by local peculiarities of parent rock or soil (Whitmore, 1972). At lower altitudes disturbance of the natural vegetation was limited and of recent occurrence, and above 1800 ft the climax forest persisted unaltered. As shown below, the isolated position of Benom has apparently prevented colonization by a few bird and mammal species found at high elevations on the Main Range or on Gunong Tahan. The degree of faunal impoverishment, however, is slight and does not materially affect the pattern of altitudinal zonation.

Although the bats collected included one undescribed species and one new to Malaya (Hill, 1972), the birds and mammals encountered were all either familiar or could be distinguished in the field and subsequently identified. It was thus possible to concentrate our efforts on the principal aim of establishing the altitudinal ranges of all species encountered. Results are presented below in the form of annotated systematic lists of birds and mammals. Patterns of distribution are examined subjectively, and have also been analysed mathematically by comparative calculations, which although simple appear to represent the first attempt to treat Malayan data on altitudinal zonation in a quantitative fashion.

METHODS

This paper is based on observations made during the Zoology Department, University of Malaya/British Museum (Natural History) expedition from 1 February –15 April 1967 (Medway, 1972) and during a subsequent return trip to Gunong Benom from 29 January to 18 February 1968. Records of occurrence summarized below are supported by evidence of several kinds, as follows:

1. Birds or bats (and one flying squirrel, *Iomys horsfieldii*) were trapped in standing mist-nets, all 12 m long by 2·4 m high with 36 mm mesh, set at low levels in the forest and open day and night. For practical reasons netting was confined to limited areas in the vicinity of each camp.

2. Small mammals were caught in traps set on the ground or on fallen logs, branches, etc. near ground level. Two types of traps were used: 50 British 'Longworth' small mammal traps, and 196 standard locally manufactured, cage-type, catch-alive traps baited with tapioca, banana or coconut flesh. All traps were set in lines, with an interval of 10 yards between traps. Trapping was most intensive around Base camp at 700–900 ft (Table 3), but traps were also set in a continuous transect in forest beside the north-east ridge path from 900–6300 ft. Six 'Special' traps designed to catch squirrels in English woodland were also tried, without success.

3. Specimens shot by day or (using a headlamp) by night.

4. Specimens caught by other means, e.g. by hand.

5. Sight-records of free-living birds or mammals by competent, experienced observers.

6. Tracks or dung.

7. Distinctive song or other vocalization.

Heights given in every case are the altitude above sea level to the nearest 100 ft of the net or trap, or of the collector or observer, ignoring the additional height of arboreal birds or mammals above ground. The heights of camps and conspicuous landmarks were established from the 1 : 63,600 map. Altitudes of intervening points were read from pocket anaeroid altimeters.

With birds, a representative collection was made of not more than twleve specimens of each species netted, the majority as rough-dried skeletons. Additional specimens surplus to requirements were ringed and released alive where caught, after being identified, measured and weighed. Surplus bats were also released alive where caught, but were not marked or banded. All animals shot or killed by other means, and all mammals trapped, were preserved as specimens; again, most were prepared as rough-dried skeletons.

All skeletons, most liquid-preserved specimens and a few skins have been deposited in the British Museum (Natural History), along with photocopies of the field records; the original field records remain with the author. Small reference collections were retained for the zoology museum of the School of Biological Sciences, University of Malaya, and for the Division of Vertebrate Zoology, Institute for Medical Research, Kuala Lumpur.

Systematic names and their colloquial English equivalents conform with Medway & Wells (in prepn.) foi birds and Medway (1969) for mammals.

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OBSERVATIONS

1. Birds

a. Resident species

Both visits by the author to Benom were made during the first quarter of the year, a period which marks the onset of the breeding season among the majority of resident terrestrial birds in Malaya (Gibson-Hill, 1952; McClure, 1968; much unpublished information in the University of Malaya Bird Ringing Project files). Observations of the reproductive condition of specimens autopsied are given in Appendix 1. In almost all adult males of every species, passerine and non-passerine, the testes were enlarged. Among females, 45 individuals representing 37 species were at or near laying condition, as indicated by the presence of at least one enlarged ovarian follicle not less than 3 mm in diameter or of an oviducal egg. Nesting by four species was observed, and dependent young of one other species were seen. Yet in the sample netted, independent juveniles formed a very small proportion of the total, even in late March and early April 1967. Moult, which follows breeding in all avian forest communities studied in Malaya (unpublished), was recorded only among nine resident forest species.

These data confirm that the birds of Benom also begin to nest at this time of year. The selective importance of altitudinal factors in the ecology of each species is presumably greater at the time of breeding than later, during dispersal of the young of the year and of post-breeding adults, and zonation will consequently be more rigid.

b. Migrants

Most migrants to Malaya during the northern winter are found in open or largely deforested country, including cleared land, marsh, swamp and foreshore. Only some 24 species (15 per cent of the total of 161 recorded migrants) occur in undisturbed forest, and their importance in the ecology of this habitat is unknown. Seven passerine species, four of which were common, and four non-passerines recorded on Gunong Benom were migratory. All proved to have a limited altitudinal zonation.

Systematic section

The records given below are shown diagrammatically in Table 1. The catches by mist-net only are summarized in Table 2.

Accipitridae

Only two specimens were collected: the Black Eagle, *Ictinaetus malayensis* at 800 ft, and the Rufous-bellied Eagle *Hieraaetus kienerii* at 1500 ft. Other observations (Table 1) are based on sight records, and probably fail to represent the true diversity and full range of diurnal raptors on Benom. The only eagle at all frequently seen and identified was the Serpent Eagle *Spilornis cheela*, recorded from 700–3600 ft.

Falconidae

A pair of Black-thighed Falconets *Microhierax fringillarius* was seen at a hole in the stump of a branch *c.* 110 ft up a tall tree, at 900 ft elevation in the disturbed forest north-east of Base camp; a further sight record was made at 1600 ft.

Phasianidae

No pheasants were seen or collected in 1967. In 1968, snare lines were set at 1500–1600 ft and 3500–3800 ft. Four Mountain Peacock Pheasants *Polyplectron inopinatum* were taken at 3500 ft near camp 3, and a Roulroul *Rollulus rouloul* and a female Great Argus *Argusianus argus* at 1600 ft. All three species undoubtedly have a greater altitudinal range. Clucking calls probably of the Mountain Peacock

Pheasant were heard one dawn at camp 4, 5000 ft. Calls attributed to the Great Argus were heard daily, from below Base camp to above camp 2½, and several display grounds were found in this range. It is not impossible that the Crested Argus *Rheinardia ocellata* was responsible for some of these, since Ulu Dong on the western slopes of Benom is one of the two localities in Malaya where this pheasant has been collected (Gibson-Hill, 1949). The display grounds of the two argus pheasants are said to be indistinguishable, and their calls very similar (Robinson, 1928). Calls of the Long-billed Partridge *Rhizothera longirostris* were heard at Base camp and at 3300–3500 ft, although no birds were seen or collected.

Columbidae

The Mountain Imperial Pigeon *Ducula badia* was common and conspicuous from camp 3 up to 6000 ft elevation. The only green pigeon identified was the Thick-billed *Treron curvirostra*, collected at 1800 ft; there were additional sight records of green pigeons, unidentified. The Little Cuckoo-Dove *Macropygia ruficeps* was the only forest bird recorded from below Base camp to above 6000 ft. At lower elevations daily flights were seen heading downhill in the morning and returning uphill each evening. The Emerald Dove *Chalcophaps indica*, although elsewhere occurring up to 4000 ft (Gibson-Hill, 1949), was found only in the vicinity of Base camp where two birds were netted.

Psittacidae

The Malay Hanging Lorikeet *Loriculus galgulus* was seen and heard by several observers from 700–3200 ft.

Cuculidae

The Indian Cuckoo *Cuculus micropterus*, identified by its distinctive call, was heard frequently from Base camp up to 2400 ft. The Large Hawk Cuckoo *C. sparverioides* was also identified by its call from 3900–5800 ft; the species has not previously been recorded from Benom, but is now presumed to be resident there. The Violet Cuckoo *Chrysococcyx xanthorhynchus* was heard and seen flying overhead once at 900 ft and several times at camp 2, and the Drongo Cuckoo *Surniculus lugubris* was found from 800–1600 ft. Four malkohas were recorded: the Black-bellied Malkoha *Phaenocophaeus diardi*, only near Base camp at 700 ft; the Chestnut-breasted Malkoha *P. curvirostris*, from 700–1700 ft; Raffles' Malkoha *P. chlorophaeus*, from the forest edge at 600 ft to the ridge below camp 2½ at 2400 ft; and the Red-billed Malkoha *P. javanicus*, from 700–2500 ft, considerably lower than the 5000 ft maximum altitude elsewhere, noted by Gibson-Hill (1949). The Greater Coucal *Centropus sinensis* was seen and collected from the track side at the forest fringe between Base camp and the Ulu Cheka Road, but did not extend to the forest proper; it is therefore excluded from Table 1.

Strigidae

Several owls were caught in mist nets at night; additional records were based on calls heard. The Mountain Scops *Otus spilocephalus* was widespread from 3500–6100 ft. This owl has previously been collected from Benom by Evans in 1923 (Chasen & Kloss, 1928), although the record was apparently overlooked by Gibson-Hill (1949). Its call—a soft, slow double hoot—in no way resembles the call of the Collared Owlet (cf. Robinson, 1928). The Reddish Scops Owl *Otus rufescens* was netted twice, at 700 ft and 5000 ft; its range is assumed to include intervening altitudes. The Collared Scops *O. bakkamoena*, was netted at 700 ft and its distinctive broken hoot was heard near camp 2. The Collared Owlet *Glaucidium brodiei* was recorded from 3600–6000 ft; its monotonous four-note call was invariably heard by day, and the one specimen netted was taken mid-morning.

Tytonidae

One female Bay Owl *Phodilus badius* was netted at night at 800 ft in disturbed forest. In addition to widespread lowland records (Gibson-Hill, 1949), Robinson (1928) has reported this owl from above 4000 ft on Fraser's Hill.

Apodidae

Six species of swifts were recorded. Of these, only the Silver-rumped Spinetail *Chaetura leucopygialis* has been listed in Table 1 since it alone appeared to have a restricted altitudinal range, with sight records from 700–1700 ft. Among the others feeding at varying heights above the canopy, the House Swift *Apus affinis* and the White-bellied Swiftlet *Collocalia esculenta* were each noted at 3600 ft (I. C. T. Nisbet); both species certainly have a more extensive altitudinal range. In February 1968, the migrant Pacific Swift *Apus pacificus* and a large spinetail *Chaetura* sp. were regularly seen high over the forest; the observers' elevation (700–2000 ft) is clearly irrelevant. In both years, the Black-nest Swiftlet *Collocalia maxima* was continuously present in large numbers, feeding above the canopy at all elevations from Base camp to the summit ridge; sight records were confirmed by a specimen netted at 6000 ft. At camp 4, 5000 ft, flocks of these swiftlets were heard flying over after dusk and before dawn although no colony was found. They were presumably roosting in a cave in the vicinity. To date, all known breeding sites of the Black-nest Swiftlet in Malaya are on off-shore islands (Gibson-Hill, 1949).

Hemiprocnidae

Only the Lesser Tree-swift *Hemiprocne comata* was recorded, from Base camp to camp 2.

Trogonidae

The two common lowland species, the Red-rumped Trogon *Harpactes duvaucelii* and Diard's Trogon *H. diardii*, were seen and collected from 700 ft and 1000 ft, respectively, up to 2500 ft. The Orange-breasted Trogon *H. oreskios*, more characteristic of submontane forest (Gibson-Hill, 1949), was seen only once at 1700 ft, and the montane Red-headed Trogon *H. erythrocephalus* was recorded from 3600–4200 ft. *H. erythrocephalus* has not previously been found east of the Main Range (Gibson-Hill, 1949).

Alcedinidae

Four red-backed Forest Kingfishers *Ceyx rufidorsus* and one black-backed *Ceyx erithacus*, were netted near the stream at Base camp. Sims (1959) has shown that the two taxa hybridise over much of their range and has suggested that they are best treated as conspecific. Since the Benom specimens were phenotypically distinct they have been listed separately. The ovary of the single female *C. erithacus* was minute and the specimen is assumed to have been a migrant (cf. Nisbet, 1968). The Chestnut-collared Kingfisher *Halcyon concreta* was netted near streams at 700 and 2500 ft, and is presumed to occur at intervening altitudes.

Meropidae

In February of 1967 and 1968 feeding flocks of Blue-throated Bee-eaters *Merops viridis* were common throughout the open country of the Cheka valley and also extended to 2200 ft in the ridge forest above camp 2. No local breeding sites were found or reported to us, and these birds were presumed to be winter visitors to the area. Despite searching, no records were obtained of Blue-tailed Bee-eater *M. philippinus*, which in the lowlands of western Selangor replaces the breeding population of *M. viridis* during the northern winter. The forest-dwelling Red-bearded Bee-eater *Nyctiornis amicta* was recorded from 1700–2700 ft.

Bucerotidae

The White-crested Hornbill *Berenicornis comatus* was recorded only in the neighbourhood of Base camp at 700 ft. Four other hornbills were conspicuous and widespread on the lower slopes of the mountain. The Wreathed Hornbill *Rhyticeros undulatus* was recorded up to 3900 ft, the Helmeted Hornbill *Rhinoplax vigil* up to 3500 ft, the Bushy-crested Hornbill *Anorhinus galeritus* up to 3400 ft, and the Rhinoceros Hornbill *Buceros rhinoceros* not above 2600 ft.

Capitonidae

The barbets as a group extended over the entire altitudinal range, within which each species proved to be restricted to a limited zone. Although few were collected, each species could be identified by at least one diagnostic call. It was thus possible to delimit accurately the altitudinal ranges of the seven species occurring on Benom.

Of five species of barbets found near Base camp, the Gaudy Barbet *Megalaima mystacophanos* had the most limited range, extending no higher than 1700 ft. The Brown Barbet *Calorhamphus fuliginosus* was noted up to 2400 ft; the Yellow-crowned Barbet *M. henricii* up to 2600 ft; the Blue-eared Barbet *M. australis* up to 2800 ft; and the Golden-whiskered Barbet *M. chrysopogon* up to 3400 ft. Of the montane group, the first to be heard on the ascent was Müller's Barbet *M.*

oorti which ranged from 2500–4000 ft, being most abundant at 3000–3500 ft. The Fire-tufted Barbet *Psilopogon pyrolophus* was recorded from 3500–6000 ft, and in a short middle section of its range was the only barbet present, between the upper limit of Müller's Barbet and the lower limit of the Golden-throated Barbet *M. franklinii* at 4400 ft. The latter extended to the summit ridge. *M. franklinii* has previously been reported from Benom (Chasen & Kloss, 1928) although the record was overlooked by Gibson-Hill (1949).

Indicatoridae

One specimen of the rare Malay Honeyguide *Indicator archipelagicus* was collected at 900 ft (cf. Medway, Nisbet & Wells, 1968).

Picidae

Woodpeckers were fairly often seen or heard at moderate and low altitudes but few were collected and visual identification was not always possible. For species recorded only once the full altitudinal range clearly remains undetermined; further experience might also be expected to add to the list. The Rufous Piculet *Sasia abnormis* was netted at 700 and 2500 ft, and the Buff-necked Woodpecker *Meiglyptes tukki* at 700 and 3600 ft; both are assumed to occur also at intervening elevations. Three lowland species were recorded more frequently: the Crimson-winged Woodpecker *Picus puniceus*, from 900–1700 ft; the Maroon Woodpecker *Blythipicus rubiginosus* from 700–3300 ft; and the Orange-backed Woodpecker *Chrysocolaptes validus* from 900–2400 ft. The following were recorded once only: the Grey-and-buff Woodpecker *Hemicircus concretus* at 700 ft; the Fulvous-rumped Woodpecker *Meiglyptes tristis* at 1700 ft; the Checker-throated Woodpecker *Picus mentalis* at 3600 ft; and the Bay Woodpecker *Blythipicus pyrrhotis* at 4900 ft, providing the first record of this species east of the Main Range (cf. Medway, Nisbet & Wells, 1968). In the montane zone, the Lesser Yellow-naped Woodpecker *Picus chlorolophus* was seen and collected at 4700–6000 ft; unconfirmed sightings at 3500 ft were tentatively attributed to this woodpecker, which again has not previously been recorded east of the Main Range (Gibson-Hill, 1949).

Eurylaimidae

Four broadbills were recorded, all at lowland elevations. One Black-and-red Broadbill *Cymbirhynchus macrorhynchos* was collected at 700 ft. The Banded Broadbill *Eurylaimus javanicus* was nesting in the tall tualang tree (*Koompassia excelsa*) at Base camp and was recorded up to 1600 ft, and the Black-and-yellow Broadbill *E. ochromalus* from 600–2300 ft. The less conspicuous Green Broadbill *Calyptomena viridis* was netted at 700, 1700 and 2500 ft.

Pittidae

One Giant Pitta *Pitta caerulea* was caught by night roosting in undergrowth at 800 ft, and one Hooded Pitta *P. sordida* was collected at 700 ft; the latter is a migratory visitor at the latitudes of Benom.

Hirundinidae

Swallows were regularly present, feeding above the canopy at all elevations from Base camp to the summit, but few positive identifications were made and the records have been omitted from Table 1. Only the migratory Barn Swallow *Hirundo rustica* was seen at the summit itself on 27 March 1967, but the resident Pacific Swallow *H. tahitica* was identified at Base camp and probably ranged higher. The damaged carcase of an Asiatic Martin *Delichon dasypus*, perhaps struck and dropped by a raptor, was picked up at 1700 ft on 15 February 1968.

Motacillidae

One Grey Wagtail *Motacilla caspica* was seen on the logging track near Base camp, 2 February 1967. The species is ecologically limited to openings in the forest habitat, and has been omitted from Table 1.

Campephagidae

The Black-faced Cuckoo-shrike *Coracina novaehollandiae* was relatively common and conspicuous from camp 3 to 5800 ft; there are no previous published records from Benom. In the lowlands, single sight records were obtained of the Lesser Cuckoo-shrike *C. fimbriata* at 1600 ft; the Black-winged Flycatcher-shrike *Hemipus hirundinaceus* at 900 ft; and the Bar-winged Flycatcher-shrike *H. picatus* at 1700 ft. Both the Fiery Minivet *Pericrocotus cinnamomeus* and the Scarlet *P. flammeus* were recorded from 700–1700 ft. The Mountain Minivet *P. solaris* was common from 3200 ft to the summit ridge above 6800 ft. Between 1700 and 3200 ft no minivets were recorded. Although further work is likely to reduce this gap there was thus no evidence of overlap between the lowland and highland species.

Aegithinidae

The Great Iora *Aegithina lafresnayei* was seen once at 700 ft. The Lesser Green Leafbird *Chloropsis cyanopogon* was recorded from 700–1700 ft; the Greater, *C. sonnerati*, once only at 900 ft; the Blue-winged Leafbird *C. cochinchinensis* over a wide altitudinal range from 700–3500 ft, and the Orange-bellied Leafbird *C. hardwickii* from 4300–4900 ft. *C. hardwickii* has not previously been reported east of the Main Range. The Fairy Bluebird *Irena puella* was common from 700–1700 ft.

Pycnonotidae

The bulbuls were well represented on Benom, common and conspicuous at most elevations. Our observations indicate a clear pattern of altitudinal zonation within the family. Of 10 species recorded below 900 ft, none were observed above 2600 ft: the Scaly-breated Bulbul *Pycnonotus squamatus* 700–1300 ft; the Grey-bellied *P. cyaniventris* 700–1800 ft; the Red-eyed Bulbul *P. brunneus*, 700–1400 ft; the White-eyed Bulbul *P. simplex*, 700–2400 ft; the Lesser Brown Bulbul *P. erythropthalmos*, 700–2500 ft; the Scrub Bulbul *Criniger bres*, 700–1800 ft; the Yellow-bellied Bulbul *C. phaeocephalus*, 700–2500 ft; Finsch's Bulbul *C. finschii*, 900–1400 ft; and the

Hairy-backed Bulbul *Hypsipetes criniger* 700–2600 ft. Two species were confined to a restricted upper lowland zone: the Crested Olive Bulbul *Hypsipetes charlottae*, below camp 2 at 1400–1700 ft where it was common, and the Streaked Bulbul *H. viridescens* (c.q. *H. malaccensis*) 1300–2400 ft. Two species had a distinctive submontane distribution: the Ashy Bulbul *H. flavala*, 1400–3600 ft, and the Ochraceous Bulbul *Criniger ochraceus*, 2500–3600 ft. The single montane species, the Mountain Streaked Bulbul *Hypsipetes macclellandii*, extended from 3500 ft to the summit ridge. The Black-and-white Bulbul *Pycnonotus melanoleucos*, previously collected at 6000 ft on Benom (Robinson, 1928), was not recorded during our expedition and has been omitted from Table 1.

Dicruridae

Two resident drongos were recorded, the Greater Racket-tailed Drongo *Dicrurus paradiseus* near Base camp at 700 ft, and the Lesser Racket-tailed Drongo *D. remifer* over a wide altitudinal range from 1600 ft, below camp 2 where birds were seen many times in February 1968, to 6000 ft. The Crow-billed Drongo *D. annectans*, one of the relatively few migratory birds of the understorey of the forest, was recorded from 1000–1800 ft in February and early March.

Oriolidae

At low elevations the Dark-throated Oriole *Oriolus xanthonotus*, was recorded at 700–800 ft, and at higher elevations the Black-and-crimson Oriole *O. cruentus* at 3100–4200 ft.

Corvidae

The Crested Jay *Platylophus galericulatus* was seen in heavily logged forest at 500 ft on the track from Base camp to Ulu Cheka, and was netted at 2500 ft. A crow collected at Base camp is identified from measurements as the rare Slender-billed Crow *Corvus enca*; a sight record at camp 2, of a single bird uttering a high-pitched caw (D. R. Wells) is also attributed to this species.

Paridae

The Sultan Tit *Melanochlora sultanea* occurred over a wide range from 700–3900 ft.

Sittidae

The Velvet-fronted Nuthatch *Sitta frontalis* was seen at 1000 and 1700 ft. The Blue Nuthatch *S. azurea*, prevously recorded from Benom by Robinson (1928), was seen once only at 5000 ft.

Timaliidae

The babblers were well represented and formed a major part of the avifauna at all elevations. Zonation was marked, with every species restricted to a limited altitudinal zone varying in range from 4000 to a few hundred feet. Seven lowland species were found only in the neighbourhood of Base camp, which may have been near the upper limit of their range: the Black-capped Babbler *Pellorneum capistratum*, Horsfield's Babbler *Trichastoma sepiarium*, the Ferruginous Babbler *T. bicolor*, the Sooty-headed Babbler *Malacopteron affine*, the Striped Wren Babbler *Kenopia striata*, the Large Wren Babbler *Napothera macrodactyla*, and the Fluffy-backed Tit Babbler *Macronus ptilosus*. Eleven others also occurring at Base camp were more widely distributed, extending to higher elevations as follows: the Short-tailed Babbler *Trichastoma malaccense*, netted at 700, 1700 and 2600 ft; the Greater Red-headed Babbler *Malacopteron magnum*, netted at 700 and 1700 ft; the Lesser Red-headed Babbler *M. cinereum*, netted at 700, 1700 and 2600 ft; the Moustached Babbler *M. magnirostre*, 700–2600 ft; the Striped Tit Babbler *Macronus gularis*, identified by its distinctive call from 700–2300 ft; the Grey-throated Babbler *Stachyris nigriceps*, 700–3600 ft; the Grey-headed Babbler *S. poliocephala*, 700–1700 ft; the White-eared Babbler *S. leucotis*, 700–2600 ft; the Red-rumped Babbler *S. maculata*, 700–1700 ft; the Red-winged Babbler *S. erythroptera*, 700–2600 ft; and the Brown Nun Babbler *Alcippe brunneicauda*, 700–2600 ft. At intermediate elevations two species were recorded in the submontane zone: the Chestnut-backed Scimitar Babbler *Pomatorhinus montanus*, 1700–2600 ft and the Small Wren Babbler *Napothera epilepidota*, from 2300 ft where a nest with downy young was found on 16 February 1968, to 3300 ft. Three others recorded at medium elevations on Benom have wider ranges elsewhere: the Marbled Wren Babbler *N. loricata* netted at 2500 ft; the Black-necked Babbler *Stachyris nigricollis*, netted at 1700 ft, and the White-bellied Yuhina *Yuhina zantholeuca*, seen from 1600–3500 ft.

In the montane zone, the Mountain Nun Babbler *Alcippe peracensis* ranged most widely, from 2600 ft where one bird was netted (establishing overlap with the lowland *A. brunneicauda*) to 6000 ft. The related but ecologically distinct Chestnut-headed Nun Babbler, *A. castaneceps*, was recorded from 3500–6000 ft. (Table 2). The three laughing thrushes also overlapped in distribution, with the rare Black Laughing Thrush *Garrulax lugubris* (not previously recorded east of the Main Range) collected at 3600 ft and seen again at 4200 ft, the Chestnut-capped Laughing Thrush *G. mitratus* recorded from 3600–5400 ft, and the Red-headed Laughing Thrush *G. erythrocephalus* from 4400 ft to the summit ridge at 6600 ft. Other birds of the lower montane zone comprised the Large Scimitar Babbler *Pomatorhinus hypoleucos* recorded from 3600 ft and ranging to the summit ridge; the Streaked Wren Babbler *Napothera brevicaudata*, the Pygmy Wren Babbler *Microura pusilla* and the Golden-headed Babbler *Stachyris chrysea*, all from 3500–6000 ft; and the Red-winged Shrike Babbler *Pteruthius flaviscapis* from 3500–5300 ft. The last named overlapped in range with the smaller, ecologically separated Chestnut-throated Shrike Babbler *P. melanotis*, recorded only at upper montane elevations from 4900–6000 ft. Also members of the upper montane fauna were the Cutia *Cutia nipalensis*, recorded from 4900–6400 ft, and the Chestnut-tailed Siva *Minla strigula*, 5200–6800 ft. Records of the Long-tailed Sibia *Heterophasia picaoides*, a noisy and conspicuous babbler, were also confined to upper montaine elevations, 4900–6500 ft, with the exception of a single bird seen at 1900 ft on 2 February 1968; this anomalous record is presumed to represent a straggler, and intervening elevations have not been included in the normal range of the species (Table 1).

Turdidae

The migratory Siberian Blue Robin *Erithacus cyane* was common in the understorey of the forest from 700–2600 ft. The latest record was a male netted on 12 April 1967, within the species' normal wintering period in Malaya (Wells, 1969). The White-rumped Shama *Copsychus malabaricus* was recorded from 700–1700 ft, where it overlapped with the Orange-tailed Shama *C. pyrropyga*, recorded from 1700–2600 ft. Along stream sides, the White-crowned Forktail *Enicurus leschenaulti* was netted only near Base camp, and the Chestnut-naped Forktail, *E. ruficapillus* at 700 and 1700 ft. In addition, an unidentified forktail was seen at 2500 ft and the distinctive thin whistle of the genus was heard at 3500 ft.

Sylviidae

Identified by its distinctive call, the Flyeater *Gerygone fusca* was recorded from 700–3200 ft. In the lower montane zone, the Chestnut-crowned Flycatcher Warbler *Seicercus castaniceps* was seen at 3500–3600 ft; this is the first record of the species east of the Main Range. At higher elevations, the Yellow-breasted Flycatcher Warbler *S. montis* was recorded from 5300–6300 ft, and the Mountain Leaf Warbler *Phylloscopus trivirgatus* from 5700–6000 ft. In both years migratory leaf warblers, *Phylloscopus* spp., were common at low to moderate elevations, feeding largely at canopy level where they were easily recognized but difficult to identify to species. The Eastern Crowned Leaf Warbler *P. coronatus* was recorded from 700–4200 ft; the Arctic Warbler *P. borealis* was positively identified only at 2700 ft but certainly has a wider range, possibly coterminous with *P. coronatus*. Near Base camp, the Red-tailed Tailorbird *Orthotomus sericeus* was found only along the track-side, nesting in the young secondary growth. The Black-necked Tailorbird *O. atrogularis* was also recorded in disturbed vegetation from 1300–1700 ft. The Mountain tailorbird *O. cuculatus* was common in virgin habitat from 4200 ft to the summit ridge at 6800 ft.

Muscicapidae

Migratory flycatchers were recorded only at lower elevations: the Brown Flycatcher *Muscicapa latirostris*, at 900–2400 ft; the Sooty Flycatcher *M. sibirica* and the Ferruginous Flycatcher *M. ferruginea*, at 1700 ft; and the Blue-throated Flycatcher *M. rubeculoides* at 700–1700 ft. Resident species recorded in this zone were the Pearl-spotted Fantail *Rhipudura perlata*, from 700–2500 ft; the Grey-headed Flycatcher *Culicicapa ceylonensis*, present over a wide altitudinal range from 700–4200 ft; the Orange-breasted Flycatcher *M. dumetoria*, netted at 700 ft; the Pale Blue Flycatcher *M. unicolor*, seen at 1500 ft; the White-throated Jungle

Flycatcher *Rhinomyias umbratilis*, from 1400–2600 ft; the Chestnut-winged Monarch *Philentoma pyrhoptera*, the Maroon-breasted Monarch *P. velatum* and the Black-naped Monarch *Hypothymis azurea*, all from 700–2500 ft; and the Paradise Flycatcher *Terpsiphone paradisi*, 1300 and 2500 ft. At higher elevations the White-throated Fantail *Rhipidura albicollis* was recorded from 3400–6800 ft. The White-throated Flycatcher *Muscicapa solitaris* was netted at 3600 ft, the first record of the species from Benom. Other resident flycatchers were common and widespread in the montane zone: the Great Niltava *Muscicapa grandis*, 4000–6000 ft; the White-fronted Flycatcher *M. hyperythra*, 4700–6700 ft; the Little Pied Flycatcher *M. westermanni*, 3800–6000 ft, and the Pygmy Blue Flycatcher *Muscicapa hodgsoni*, 3500–6000 ft.

Nectariniidae

Near Base camp the Little Spiderhunter *Arachnothera longirostris* was netted in greater numbers than any other bird (Table 2). The local abundance of this long-billed nectarivore was undoubtedly related to the proliferation of wild banana plants, many in flower, along the tracks and in other areas disturbed by recent logging operations; however its full altitudinal range from 700–3600 ft extended into virgin forest near camp 3. The Grey-breasted Spiderhunter *A. affinis* was recorded from 700–1700 ft, and the Purple-naped Sunbird *Hypogramma hypogrammicum* from 700–3800 ft. A male Scarlet Sunbird *Aethopyga mystacalis* was seen at 700 ft, and the Plain Sunbird *Anthreptes simplex* and the Ruby-cheeked Sunbird *A. singalensis* were both recorded at 1700 ft. The Long-billed Spiderhunter *Arachnothera robusta* was seen at 1400 ft, and an unidentified yellow-cheeked spiderhunter at 800 ft. At higher elevations, the Black-throated Sunbird *Aethopyga saturata* was recorded from 3500–6700 ft, and the Streaked Spiderhunter *Arachnothera magna* from 3600–5000 ft.

Dicaeidae

The Orange-bellied Flowerpecker *Dicaeum trigonostigma* was recorded only at 700 ft, but the Yellow-throated Flowerpecker *Prionochilus maculatus* was seen and netted from 700–3500 ft. At higher elevations the Fire-breasted Flowerpecker *Dicaeum ignipectus*, not previously recorded from Benom, was seen from 3500–5700 ft. One Thick-billed-Flowerpecker *D. agile* (=*Piprisoma modestum* in Gibson-Hill, 1949; cf. Salomonsen, 1960) seen at 4200 ft (I. C. T. Nisbet) constitutes a new locality record for this rare bird.

Zosteropidae

White-eyes seen from 1600–3600 ft are attributed to *Zosterops everetti*.

Fringillidae

The Brown Bullfinch *Pyrrhula nipalensis* was common from 5000–6100 ft.

2. Mammals

It is unlikely that there are major seasonal changes in altitudinal zonation among the terrestrial mammals of the Malaysian forest, with the possible exception of some bats. The commoner rats have been shown to be permanently resident within small ranges throughout their lifetimes (Harrison, 1958). Work on rats and other small mammals in Selangor has found no limited breeding season, although some species show seasonal peaks in reproductive activity (Harrison, 1955; Medway, 1967). The evidence of autopsied specimens from Benom (Appendix 2) shows that a large proportion of females collected were pregnant or lactating at the time of the expedition.

Middle-sized mammals including siamang (Chivers, 1971), gibbons (Ellefson, 1968), leaf-monkeys (Furaya, 1962; Bernstein, 1968), macaques (Bernstein, 1967) and mouse-deer (unpublished), either as small family groups or large gregarious troops, also reside permanently within the bounds of restricted territories or home-ranges. Among the bigger ungulates, elephant (Mohamed Khan, 1967), rhinoceros (Strickland, 1966) and gaur (Hubback, 1937; Weigum, 1970) have also been shown to forage within the limits of large but circumscribed ranges.

Among the bats, no Malayan species is known to be migratory, although several —including members of the families Pteropodidae, Rhinolophidae and Vespertilionidae—make long flights in search of food, while others shift roosting sites irregularly or at certain stages of the reproductive cycle (cf. Medway, 1969). Autopsy records summarized in Appendix 2 show that the majority of females of most species of bats taken during the expedition were pregnant or lactating. As among birds, it is likely that the selective effect of factors controlling altitudinal zonation is strongest at the time of production of young. Although fruit bats were trapped in standing mist-nets left untended during the night, all rhinolophids and vespertilionids were netted at dusk shortly after emergence, and must have been close to their roosts; the single emballonurid species was taken actually at its roost sites.

In contrast to birds, among which sight records and call identifications form a major proportion of the observations summarized above, most small mammals (except the diurnal squirrels) are inconspicuous, often nocturnal or difficult to see by day. The majority of records given below are therefore based on specimens collected, and in many cases fail to indicate the species' full altitudinal range. Except for readily caught and common diurnal squirrels and ground-living rats, even trapping results are deficient. The 'Longworth' traps caught only one small rat, *Rattus whiteheadi*, in a total of 1500 trap nights, and are evidently unsuitable in this environment. With the exception of the shrews *Crocidura fuliginosa* and *Suncus etruscus*, which may be very rare in virgin forest, there are few mammals in the Malaysian rainforest small enough to enter this type of trap. Even the standard cage traps were relatively unsuccessful. The overall rate of catch, at 2·0 per 100 trap nights was low (Table 3, cf. Harrison's figure of 5·0/100 trap nights from Selangor forests, given by Medway, 1966). Of 20 species trapped, five (25 per cent) were taken only once and not recorded by any other means; their full altitudinal range is certainly greater than indicated.

Systematic section

See Table 4 for diagrammatic summaries of distribution.

Erinaceidae

The Moonrat or Gymnure *Echinosorex gymnurus* was trapped once near Base camp; this species is characteristically present only at low density in lowland forest (Harrison, 1969).

Soricidae

A shrew, presumably the South-east Asian White-toothed Shrew *Crocidura fuliginosa*, was seen at camp 4 but not caught.

Cynocephalidae

The nocturnal Flying Lemur or Colugo *Cynocephalus variegatus* was collected only near Base camp.

Pteropodidae

All fruit bats were netted and records are therefore confined to the areas near each camp in which nets were set. Three Malaysian Fruit Bats *Cynopterus brachyotis* were taken at Base camp and camp 2 only. The Dusky Fruit Bat *Penthetor lucasi* was netted once, at Camp 3. This species is an obligatory cavernicole and its distribution is presumably limited by the occurrence of suitable caves or rock shelters in which it can roost; as already noted (Medway, 1972), such sites are abundant at higher altitudes on Benom. Four Spotted-winged Fruit Bats *Balionycteris maculata* were taken, at Base camp and camp 2. Two Tailless Fruit Bats *Megaerops ecaudatus* and two Hill Long-tongued Fruit Bats *Macroglossus minimus* were netted near Base camp; both species have a wider altitudinal range elsewhere in Malaya (Medway, 1969). The Black-capped Fruit Bat *Chironax melanocephalus* was taken from 900–5000 ft, most specimens at 3500 ft and upwards. The Grey Fruit Bat *Aethalops alecto* was taken only at 6000 ft on the ridge above camp 5; the species has not previously been recorded east of the Main Range in Malaya (Hill, 1961).

Emballonuridae

Small groups of Sheath-tailed Bats *Emballonura monticola* were found at roost under the trunks of fallen trees at 900 and 1600 ft.

Rhinolophidae

At Base camp and camps 2 and 2½, the three horseshoe bats *Rhinolophus affinis*, *R. stheno* and *R. refulgens* were netted in large numbers at nightfall from mixed flight streams winding through the forest a few feet above ground; no roosting sites could be found. Both sexes were represented in the samples in approximately equal numbers; most females were pregnant (Appendix 2) but evidently not segregated in maternity colonies. *Rhinolophus macrotis* was also taken at Base camp, but was proportionally more abundant at 2500 and 3500 ft; the species had not previously been recorded from Malaya (Hill, 1972).

The Trefoil Horseshoe Bat *Rhinolophus trifoliatus* and the three roundleaf horseshoe bats *Hipposideros bicolor*, *H. galeritus* and *H. diadema* were netted only near Base camp.

Vespertilionidae

Single specimens of the rare *Pipistrellus ridleyi* and the new species *P. societatis* (Hill, 1972) were netted in tall forest under a closed canopy near Base Camp. *P. javanicus* was taken near camp 2; elsewhere this pipistrelle has been found in the settled lowlands, and in a few towns it is locally common (Medway, 1969). Of the tube-nosed bats, *Murina cyclotis* was netted near Base camp and *M. huttoni* at 4800 ft; the latter had not previously been found in Malaya (Hill, 1972). The Papillose Bat *Kerivoula papillosa* was taken at 1700 and 2500 ft.

Tupaiidae

One Lesser Treeshrew *Tupaia minor* was trapped at 800 ft, and one Pentail Treeshrew *Ptilocercus lowii* shot at 1700 ft. The Common Treeshrew *Tupaia glis* was seen from 900–3000 ft, although collected only at 1700 ft (B. L. Lim).

Lorisidae

One Slow Loris *Nycticebus coucang* was collected at 800 ft.

Cercopithecidae

The commonest monkey at lower elevations was the Dusky Leaf-monkey *Presbytis obscura*, seen and collected from 700–2800 ft. The Banded Leaf-monkey *P. melalophos* was also present at these altitudes, and extended up to the final slopes of the summit where a large troop was disturbed at midday at 6500 ft. During the expedition, the Long-tailed Macaque *Macaca fascicularis* was recorded only at 700 ft; a sight record above 4000 ft on Benom has since been reported to me, but is not included in Table 2. Similarly, during the expedition Pig-tailed Macaques *M. nemestrina* were found only at 2400 and 3600 ft, but elsewhere the altitudinal range of the species is greater and includes lowland forest (Bernstein, 1967).

Hylobatidae

The Lar Gibbon *Hylobates lar* was seen or heard from Base camp to 4700 ft and the Siamang *Hylobates syndactylus* over a wider range, up to the saddle between camp 5 and the summit ridge, at 6000 ft. Both species evidently exploit a broad variety of forest types, and are not restricted to the lowland formations dominated by dipterocarps.

Manidae

The Pangolin *Manis javanica* was collected once near Base camp.

Sciuridae

Apart from the large primates and several ungulates, the Slender Squirrel *Sundasciurus tenuis* is the only mammal common both at Base camp and up to 6000 ft on the summit ridge. On Gunong Tahan a high-level subspecies, *S. tenuis tahan* (Bonhote), has been distinguished; examination of the material from Benom suggests that no parallel local subspeciation has occurred. Although no records of this squirrel were obtained between 1900 and 4400 ft, it is assumed that it occurs continuously through the full altitudinal range.

All other typical (diurnal) squirrels exhibit marked altitudinal zonation. The Golden-backed Squirrel *Callosciurus caniceps* was collected only once, below Base camp. The species is ecologically restricted to disturbed forest, secondary growth and plantation, and therefore excluded from the virgin forest higher on Benom; in other localities however, where ecological conditions permit, it has been found at greater altitudes (Medway, 1969). Of the squirrels inhabiting undisturbed forest, the following were recorded at low altitudes only: the Plantain Squirrel *Callosciurus notatus* and the Black-banded Squirrel *C. nigrovittatus* from 700–1100 ft; Prevost's Squirrel *C. prevostii* at 1700 ft; the Horse-tailed Squirrel *Sundasciurus hippurus* collected at 800 ft; Low's Squirrel *S. lowii* from 800–1200 ft; the Three-striped Ground Squirrel *Lariscus insignis* from 700–1200 ft, and the Shrew-faced Ground Squirrel *Rhinosciurus laticaudatus* at 700–800 ft only. There was a distinct gap between the upper records of this lowland group and the lower limits of the two highland species, the Belly-banded Squirrel *Callosciurus flavimanus* at 4000 ft and the Himalayan Striped Squirrel *Tamiops macclellandii* at 3600 ft. Both *C. flavimanus* and *T. macclellandii* were common and conspicuous within their range, extending to at least 6000 ft.

Of the flying squirrels, the Red-cheeked Flying Squirrel *Hylopetes spadiceus* and the Smoky Flying Squirrel *Pteromyscus pulverulentus* were collected at 1700 ft; Horsfield's Flying Squirrel *Iomys horsfieldii* was trapped several times at 800 ft near Base camp where it was evidently common, and once caught in a mist-net at 5100 ft. The Black Flying Squirrel *Aeromys tephromelas* was collected at 700 and 2500 ft; the Red Giant Flying Squirrel *Petaurista petaurista* was common from 700–1500 ft; and the Spotted Flying Squirrel *P. elegans* was collected only at 700–800 ft. Elsewhere *P. elegans* has an extensive high altitude range (Harrison, 1964; Medway, 1969). Further collecting may find it higher on Benom, but the present records emphasize that the species is not the montane ecological counterpart of *P. petaurista.*

Muridae

The small arboreal mouse *Chiropodomys gliroides* was seen at Base camp and collected at 1700 ft (B. L. Lim). Of the true rats, genus *Rattus*, Mueller's Rat *R. muelleri* and Bowers's Rat *R. bowersii* were trapped only near Base camp (Table 3). Elsewhere the latter in particular has a more extensive altitudinal range. Both species, however, are ecologically restricted to valley bottoms (cf. Harrison, 1957), a habitat that was adequately sampled only below 1000 ft. At higher elevations all traps were set on the crest or flanks of the north-east ridge, from which *R. muelleri* and *R. bowersii* would be ecologically excluded. The Dark-tailed Tree Rat *R. cremoriventer* was also trapped only near Base camp. The commonest rat at lowland elevations was the Long-tailed Giant Rat *R. sabanus* (cf. Table 3), which was trapped from 700–2900 ft. Whitehead's Rat *R. whiteheadi* and the Brown Spiny Rat *R. rajah* were both trapped from the vicinity of Base camp up to 2500 ft. The Red Spiny Rat *R. surifer* was trapped once only, at 2500 ft, and was greatly outnumbered in the catch by its sibling species *R. rajah* (Table 3); the affinity of these rats is discussed below by Yong (1969, 1972). Near camp 3, we trapped one young adult female Malaysian Wood Rat *R. tiomanicus*, a species which on the Malayan mainland is semi-commensal in habit and characteristically found in disturbed or fringing forest, secondary growth and plantation. Island populations of this rat occupy a wider variety of habitats (Medway, 1966), and the occurrence of this specimen here on Benom indicates that on the mainland, too, virgin forest is not a complete barrier to the dispersal of the species.

With this exception, no overlap in range was found between the lowland rats and the two highland species, the Malayan Mountain Spiny Rat *R. inas* and Edwards's Giant Rat *R. edwardsi*, neither of which was trapped below 3500 ft. Both occurred up to at least 6000 ft (Table 3).

Hystricidae

Spines of the Brush-tailed Porcupine *Atherurus macrourus* were found in the dung of a large carnivore (tiger or leopard) at 1900 ft. There were no other records of porcupines.

Ursidae

Tracks or other traces of the Malay Sun Bear *Helarctos malayanus* were found from near Base camp up to 2400 ft; a single bear was seen 1600 ft (R. Garcia).

Viverridae

A Banded Linsang *Prionodom linsang* was caught in a ground snare at 3500 ft. A Binturong *Arctictis binturong* was collected at 700 ft and a Banded Palm Civet *Hemigalus derbyanus* at 800 ft. Slightly more common near Base camp was the Three-striped Palm Civet *Arctogalidia trivirgata*, shot and seen from 900–1200 ft.

Felidae

The Leopard Cat *Felis bengalensis* was recorded several times near Base camp only. The Tiger *Panthera tigris* and Leopard *P. pardus* were positively identified from tracks only near Base camp, but indistinct tracks and the dung of large felids were found at several points up to 5500 ft.

Elephantidae

Tracks and other signs of the Indian Elephant *Elaphas maximus* were numerous in the valley by and below Base camp, but there was no sign that they went any higher.

Tapiridae

The entire length of the path from Base camp virtually to the summit was marked with old and fresh tracks and dung of the Malay Tapir *Tapirus indicus*. At no point was there evidence of more than one animal passing at a time, and all traces were compatible with the presence of a single adult tapir ranging very widely on the mountainside.

Suidae

Pig tracks were found from 700–5300 ft, but no animals were seen. The species is likely to be the common Wild Pig, *Sus scrofa*, which has been collected in the south-east sector of the Kerau Game Reserve (Hoogstraal *et al.*, 1972). There are however, unconfirmed reports of the Bearded Pig *S. barbatus* from Kuala Tahan, Sungei Tembiling, north of Benom in the Pahang drainage (Medway, 1963), and without specimens the tracks alone cannot distinguish between the two species.

Tragulidae

The Lesser Mouse-deer *Tragulus javanicus* was collected near Base camp, where tracks were also identified, and seen once at 6000 ft (B. Hamid).

Cervidae

The Barking Deer *Muntiacus muntjak* was identified from tracks near Base camp. Elsewhere this deer has been shown to have a wide altitudinal range (Medway, 1969).

Bovidae

A Serow *Capricornis sumatraensis* was seen in the stream bed at Base camp, and tracks were identified at 2600 ft. In general the Serow frequents steep, damp gullies in the Malayan hills, and may be ecologically excluded from the high ridges that the expedition followed.

DISCUSSION

1. The lowland fauna

Of 191 species of birds identified in the forest on Gunong Benom, 141 species

(74 per cent of the total) were recorded at altitudes below 2500 ft (Table 1), and of 81 species of mammals, 69 (85 per cent) were recorded within this range (Table 4).

For both classes, the composition of the lowland fauna is similar to assemblages of species from forest at comparable altitudes in Selangor, on the western side of the Main Ridge, e.g. the birds of Ampang Forest Reserve (Medway & Wells, 1963; K. W. Scriven, unpublished), or Ulu Gombak Forest Reserve (Medway & Wells, 1964; McClure, 1966, 1967; Medway, unpublished), and the mammals of Sungei Buloh Forest Reserve (Harrison, 1969). Evidently the Main Range, with several passes lower than 2500 ft at its southern end, does not form a barrier to the distribution of lowland birds or mammals in this region.

Even within the lowlands below 2500 ft, progressive attenuation of the fauna is observed in both classes. Thirty species of birds and 29 mammals were recorded only below 1000 ft. A few of these (e.g., the rodents *Callosciurus caniceps* and *Rattus muelleri*) are known to be ecologically restricted to habitats that did not occur or were not sampled above this altitude; others were difficult to collect or observe, or rare or widely dispersed species, poorly represented in our sample and likely to occur in fact over a greater altitudinal range. But, particularly among the birds for which data are more comprehensive, a proportion of these restricted lowland species must have been near the natural upper limit of their range at the altitude of Base camp.

The progressive reduction in the number of species with altitude even within the lowland range is shown in Tables 5 and 6, in which it is seen that 109 birds and 62 mammals were recorded below 1000 ft, 112 birds and 40 mammals between 1000–1900 ft, and only 70 birds and 25 mammals in the range 2000–2900 ft.

Beyond 2500 ft, upward extension of both lowland faunas is limited. The effect is again more marked among birds of which only 24 lowland species reached 3000 ft and only four were recorded at 4000 ft; only one forest bird, the cuckoo-dove *Macropygia ruficeps*, extended over the entire altitudinal range explored, from 700 ft to the summit ridges above 6000 ft. Among mammals only 15 lowland species reached 3000 ft, but of these nine extended to 4000 ft or above and effectively had no altitudinal limits.

It is of interest to note that the lowland fauna included all migrant birds, although there is variation in the altitudinal limits of each species. The commoner species for which reliable data were obtained included the flycatcher *Muscicapa rubeculoides* (700–1700 ft), the robin *Erithacus cyane* (700–2600 ft) and the leaf warbler *Phylloscopus coronatus* (700–4200 ft). Several *E. cyane*, ringed and later retrapped in the same area, were clearly sedentary in their winter quarters, and repeated sight records of *Muscicapa latirostris* and *M. sibirica* at distinctive perches indicated that these flycatchers, too, were sedentary. All migratory passerines recorded on Benom have been trapped during their migration at much higher elevations (cf. Medway, Nisbet & Wells, 1968; Nisbet, 1968). Evidently they do not remain at these heights, but disperse to winter in the forest at lower elevations.

The catch of birds in mist-nets gives an indication of the number of species active in the undergrowth and lower storey of the forest, and therefore susceptible to this method of trapping. At lowland elevations (below 2000 ft), 55 species were netted, representing 39 per cent of the total number recorded. Some ground-living birds (e.g. gallinaceous birds, and the pittas) may be too large or too wary to be netted; a few others within this vertical zone may be too small to have been held in the mesh of the net. Field observations, however, support the indication that about three-fifths of the lowland avifauna is active in the middle and upper storeys of the forest, above the level of the mist-nets.

In a normal ringing survey, in which birds are not abstracted from the population, netting results also serve as a guide to the comparative abundance of birds in the forest undergrowth. Since a large proportion of the birds netted on Benom were killed for museum specimens, figures obtained are not comparable. Despite this, the average numbers of birds/net/day below 2000 ft (Table 2) are higher than the catches in lowland forest at Subang, Selangor, which varied from 0·83 to 0·46 during the course of the year (McClure & Othman, 1965). The high catch near Base camp on Benom is attributable to the large numbers of Little Spiderhunters netted (Table 2); if these are excluded the mean number of birds/net/day is 1·0.

2. The highland fauna

As shown above, only a very small proportion (3 per cent) of the lowland birds reach 4000 ft, and the avifauna of the upper 2000 ft of the mountain is very distinct. Only 48 species were found above 4000 ft, of which 39 reach 5000 ft and 31 reach 6000 ft (Table 5). Compared with the highland avifauna of the Main Range, the list of species from Benom is slightly impoverished. The following montane birds are relatively common and conspicuous at Fraser's Hill on the Main Range, and are unlikely to have been missed if present on Benom; those marked * are recorded from Gunong Tahan (Ogilvy-Grant, 1908; Gibson-Hill, 1949): *Picus flavinucha, Kitta chinensis**, *Trichastoma tickelli, Leiothrix argentaurus**, *Minla cyanouroptera, Myiomela leucura* and *Brachypteryx leucophrys.* Also absent is *Prinia atrogularis*, known in Malaya only from Gunong Tahan where it is common in the stunted, open vegetation of the high plateaux.

Among mammals, also, the highland fauna above 4000 ft was impoverished. But many larger species ranged from the lowlands high into the montane zone, and only four small rodents were restricted to altitudes above 3500 ft. Again two conspicuous mammals, common at Fraser's Hill, are unlikely to have been missed if present on Benom: *Hylomys suillus, Dremomys rufigenis.* Only the latter is found on Gunong Tahan (Bonhote, 1908).

The faunal differences between Benom and Tahan indicate that each mountain was independently colonized from a different source by a slightly different community of montane birds and mammals. The area of high ground on Benom is relatively extensive, estimated as 75 square miles above 3000 ft (Medway, 1972). Unless the local extinction of montane species has occurred in recent times, the narrow strip of lowlands *ca.* 20 miles wide has evidently been a partial barrier to the distribution of specialized high altitude forms from the Main Range.

In the upper 2000 ft of the mountain, near camps 5 and 6, 22 species of forest birds were taken in mist nets out of a total fauna of 41 species (53 per cent). The increased proportion of the avifauna susceptible to netting can be correlated with the reduced height of the forest at these altitudes (Whitmore, 1972), and consequent limitation on vertical separation of bird species. The overall rate of trapping, as birds/net/day, was lower than at Base camp and camp 2, but not below the mean figure for lowland forests at Subang, Selangor (McClure & Othman, 1965).

Among birds, the high ridges above 6000 ft are occupied merely by a depleted selection of the species present at 5000 ft, and there is no evidence of a distinct summit fauna. Among mammals, however, the fruit bat *Aethalops alecto* was found only in this zone, to which it is apparently specialized (Hill, 1961).

3. The intermediate fauna

Most birds recorded between 2000–3900 ft are clearly distributed mainly in the highlands or mainly in the lowlands (Table 1). The transition between two zones occurs relatively abruptly between 2500 and 3500 ft, and thus corresponds to the floral boundary between Lowland Rain Forest and Lower Montane Rain Forest (Whitmore, 1972). Among mammals a similar transition is seen at this altitude in rodents, of which the highland and lowland faunas are very distinct (Table 4).

Among the birds but not among the mammals (with the possible exception of one fruit bat, *Chironax melanocephalus*) a few species are restricted in their distribution to middle altitudes. Adequately attested examples include the trogon *Harpactes erythrocephalus*, Mueller's Barbet *Megalaima oorti*, the bulbuls *Criniger ochraceus*, and *Hypsipetes flavala*, the oriole *Oriolus cruentus*, and the wren-babbler *Napothera epilepidota*. Only three of these, however (*M. oorti*, *C. ochraceus* and *N. epilepidota*) are strictly intermediate in altitudinal zonation, covering the 2500-3500 ft range, and the assemblage does not form a coherent fauna.

Ninety-nine species of birds and 31 species of mammals were identified within the 2000–3900 ft zone of the mountain. Despite its mixed nature this assemblage contains only about two-thirds the number of species recorded near Base camp. Forty-seven species of birds were netted at camps 2½ and 3, indicating that just under half the avifauna was active in the lower storey of the forest. The numbers of birds/net/day at both sites was similar to catches at other altitudes (Table 2).

4. Quantitative comparisons

The preceding subjective examination of the occurrence of birds and mammals on Benom has confirmed that (as expected) there are two main altitudinally exclusive faunas represented in both classes, namely a highland fauna and a lowland fauna, which meet at an intermediate zone where much overlapping occurs and where among birds a few distinctive middle-altitude species are found. It is also clear that this broad pattern is complicated and partly obscured by differences in the distributions of member species of each fauna, which do not all have common altitudinal limits. The most notable overall trend is a progressive reduction in number and diversity of species with increasing altitude.

Two coefficients used by ecologists to compare samples from different areas in terms of the species present can be applied to this situation. One is Jaccard's *coefficient of community*, defined as the number of species common to two areas, expressed as a percentage of the total number of species. More widely used is Soerensen's coefficient, in which the number of species common to the two areas is expressed as a percentage of the mean number of species per area (Greig-Smith, 1964 : 136).

For this comparison, the mountainside can conveniently be divided along the thousand feet contours into seven altitudinal zones. In Tables 5 and 6, the number of species recorded in each zone, the number common to all pairs of zones and the

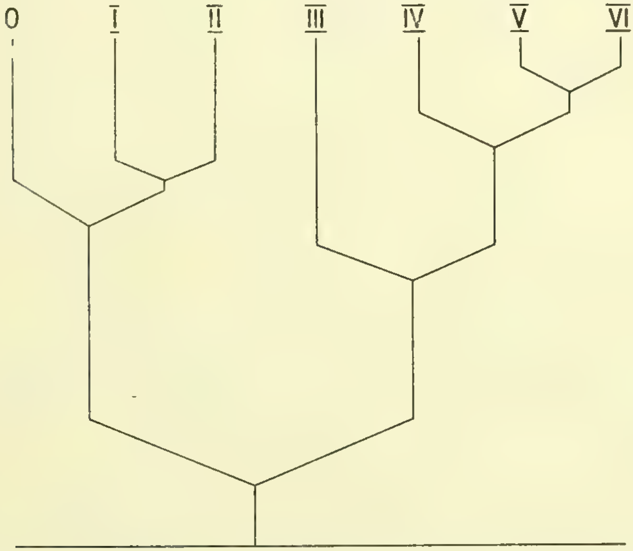

Fig. 1. Dendrogram of Soerensen's coefficient calculated for all birds recorded on Benom in successive altitudinal zones, indicated as follows: 0 = 600–900 ft, I = 1000–1900 ft, II = 2000–2900 ft, III = 3000–3900 ft, IV = 4000–4900 ft, V = 5000–5900 ft, VI = 6000–6916 ft. The heights of the points of furcation above base line are proportional to the combined coefficients.

total present in any combined pair of zones have been recorded. In Table 7, Soerensen's coefficient has been calculated for all possible pairs of zones, for both classes.

The same results can be presented graphically in the form of dendrograms (Figs 1 and 2), obtained by nearest-neighbour sorting of the coefficients expressed in Table 7. This presentation *inter alia* emphasizes the relatively greater distinctiveness of the middle zone (III) among birds, and the greater divergence of highland and lowland faunas among birds compared with the mammals.

These analyses, in terms only of species present, remain crude and far from ideal without reference to variations in the abundance of species at different altitudes. Unfortunately, the means by which distributions were gathered in most cases were too diverse for any reliable quantitative assessment of population densities to be made. The only example of a single technique applied reasonably consistently at all altitudes is mist-netting for birds. Although there are many imponderables, the catches per net/day of any particular species can be taken to indicate broadly its abundance at different altitudes.

By this criterion, certain birds were definitely rarer near the limits of their altitudinal range than at its centre, as illustrated by the catches of the three species of *Alcippe* (Table 2). Although the actual numbers caught are not directly comparable, lists from the different netting areas can be made which rank the species

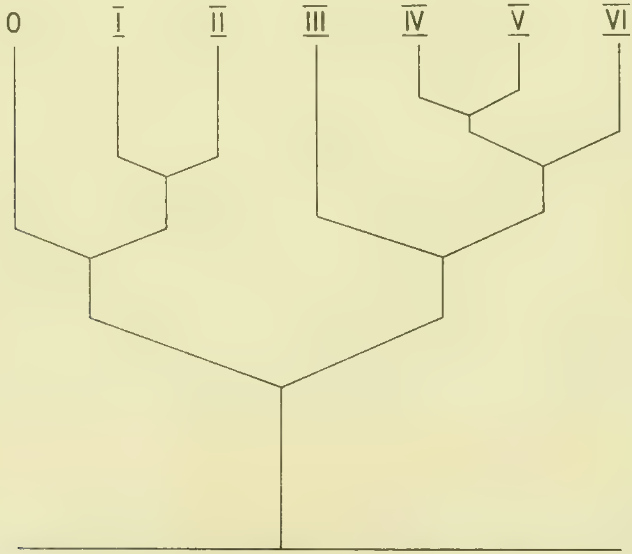

FIG. 2. Dendrogram of Soerensen's coefficient calculated for the mammals of Gunong Benom. Conventions as for Fig. 1.

taken in order of frequency, i.e. the number of individuals netted, with zero ranking if not netted. From these ranked lists the coefficient τ can be derived (Kendall, 1955). In Table 8, values of τ computed for each netting area are given, and in Fig. 3 the corresponding dendrogram again obtained by nearest-neighbour sorting. In these results, the avifaunas sampled by netting near the forest floor are shown to be even more distinctly zoned than indicated by the wider lists including canopy species.

The implications of this difference, and the broader problem of the factors controlling altitudinal zonation, remain the subject of more intensive ecological research which, it is hoped, later visitors to Benom may have the opportunity to pursue.

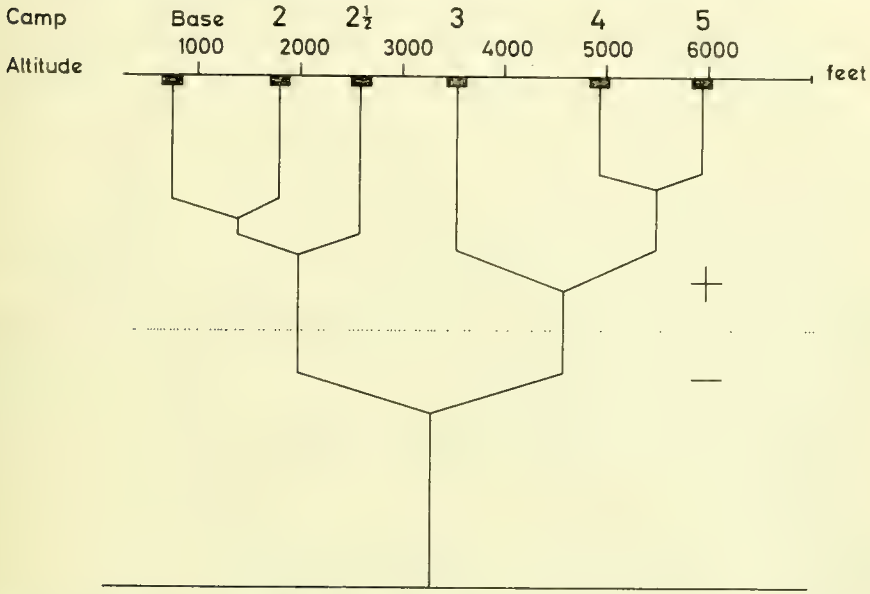

FIG. 3. Dendrogram of τ for ranked lists of birds netted at five stations on Gunong Benom.

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APPENDIX 1

Breeding and moult among birds on Gunong Benom, 11 February–15 April 1967. Observations on breeding are based on specimens autopsied. Females were considered to be in breeding condition if any follicle was 3 mm or more in diameter, or if an egg was found in the oviduct.

Species No.	Species	FEMALES No.	FEMALES Weights (g) Mean	FEMALES Weights (g) Range	FEMALES Wing (mm) Mean	FEMALES Wing (mm) Range	FEMALES Reproductive condition No. ex'd	FEMALES Reproductive condition No. in breeding cond'n	MALES No.	MALES Weights (g) Mean	MALES Weights (g) Range	MALES Wing (mm) Mean	MALES Wing (mm) Range	MALES Testis length (mm) No.	MALES Testis length (mm) Mean	MALES Testis length (mm) Range
1.	*Ictinaetus malayensis*	1	—	930	—	530	—	—	—	—	—	—	—	—	—	—
10.	*Ducula badia*	1	—	455·5	—	220	—	—	1	—	414·1	—	233	1	—	14
11.	*Treron curvirostris*	—	—	—	—	—	—	—	1	—	149·2	—	134	1	—	16
12.	*Macropygia ruficeps*	1	—	92·0	—	141	—	—	2	—	70·3, 82·1	—	140, 142	2	—	10, 10·5
13.	*Chalcophaps indica*	2	—	—, 110·0	—	142, 148	2	0	—	—	—	—	—	—	—	—
18.	*Surniculus lugubris*	1	—	40·0	—	140	1	0	—	—	—	—	—	—	—	—
19.	*Phaenicophaeus diardi*	—	—	—	—	—	—	—	1	—	72·2	—	132	1	—	5
20.	*Phaenicophaeus curvirostris*	1	—	167·6	—	172	1	0	—	—	—	—	—	—	—	—
21.	*Phaenicophaeus chlorophaeus*	—	—	—	—	—	—	—	2	—	49·8, 52·4	—	117, 112	1	—	4
22.	*Phaenicophaeus javanicus*	1	—	133·5	—	150	1	1	4	108·8	100·3–122·1	144·3	141–147	4	4·5	4–5
23.	*Otus rufescens*	—	—	—	—	—	—	—	2	—	43·2, 86·4	—	130, 132	2	—	5, 7
24.	*Otus spilocephalus*	2	—	66·6, 93·8	—	134, 139	2	2	4	59·0	55·3–63·4	135·8	133–140	4	6·5	5·5–7
25.	*Otus bakkamoena*	—	—	—	—	—	—	—	1	—	101·2	—	148	1	—	6·5
26.	*Glaucidium brodiei*	—	—	—	—	—	—	—	1	—	58·1	—	87	1	—	5·5
27.	*Phodilus badius*	1	—	230·0	—	191	1	0	—	—	—	—	—	—	—	—
30.	*Harpactes diardii*	1	—	106·1	—	149	1	1	1	—	107·3	—	144	1	—	4
32.	*Harpactes duvaucelii*	2	—	35·5, 40·0	—	103, 115	2	1	3	38·1	36·4–39·3	107·3	106–108	2	—	4, 4
33.	*Harpactes erythrocephalus*	1	—	86·6	—	145	1	1	—	—	—	—	—	—	—	—
35.	*Ceyx rufidorsus*	1	—	16·5	—	59	1	0	2	—	16·8, 17·6	—	61, 62	2	—	5, 5
34.	*Ceyx erithacus*	1	—	14·7	—	59	1	0	—	—	—	—	—	—	—	—
36.	*Halcyon concreta*	2	—	72·6, 77·4	—	109, 113	2	1	3	65·9	60·1–72·3	107·0	107 (all)	3	5	5
38.	*Nyctiornis amicta*	—	—	—	—	—	—	—	1	—	74·4	—	130	1	—	2·5
44.	*Psilopogon pyrolophus*	1	—	145·3	—	129	1	1	1	—	135·5	—	123	1	—	5
45.	*Megalaima chrysopogon*	1	—	185·6	—	127	1	1	2	—	173·1, 180·0	—	127, 128	2	—	10, 7
47.	*Megalaima franklinii*	1	—	64·9	—	98	1	0	2	—	61·4, 73·3	—	97, 99	2	—	6, 7
48.	*Megalaima oorti*	3	73·0	71·1–77·4	96·0	95–97	3	2	—	—	—	—	—	—	—	—
49.	*Megalaima henricii*	1	—	78·1	—	92	1	0	2	—	68·4, 72·6	—	100, 108	2	—	8, 10
50.	*Megalaima australis*	—	—	—	—	—	—	—	1	—	33·8	—	77	1	—	10
51.	*Calorhamphus fuliginosus*	2	—	43·9, 46·5	—	80, 102	2	0	1	—	48·4	—	83	1	—	0
53.	*Sasia abnormis*	1	—	10·4	—	50	1	1	1	—	7·4	—	54	1	—	3
57.	*Meiglyptes tukki*	1	—	47·4	—	111	1	0	1	—	47·4	—	103	1	—	< 1
[illegible]	*Blythipicus rubiginosus*	1	—	71·0	—	111	1	0	0	—	—	—	—	—	—	—

63.	*Calyptomena viridis*	2	—	44·1, 54·1	—	103, 99	2	0	5	52·2	47·5–54·3	101·0	97–104	5	15·8	12–18
64.	*Cymbirhynchus macrorhynchos*	0	—	—	—	—	—	—	1	—	59·4	—	104	1	—	2
66.	*Eurylaimus javanicus*	1	—	74·3	—	102	1	0	1	—	78·5	—	105	—	—	—
67.	*Pitta caerulea*	0	—	—	—	—	—	—	1	—	202·0	—	155	1	—	4
70.	*Coracina novaehollandiae*	2	—	92·1, 92·9	—	162, 160	2	1	3	91·6	88·0–98·3	164·0	163–165	3	7·0	6–8
73.	*Pericrocotus solaris*	3	15·5	15·4–15·6	79·7	78–83	3	0	3	14·3	13·5–15·1	79·1	73–84	2	8·0	7–9
75.	*Pericrocotus flammeus*	0	—	—	—	—	—	—	1	—	24·4	—	85	1	—	8
78.	*Chloropsis cyanopogon*	1	—	19·1	—	80	1	1	2	—	22·7, 22·8	—	91, 85	2	—	7, 8
80.	*Chloropsis cochinchinensis*	0	—	—	—	—	—	—	1	—	25·0	—	86	1	—	3
82.	*Irena puella*	1	—	67·4	—	117	1	1	2	—	75·6, 75·7	—	127, 124	2	—	11, 12
83.	*Pycnonotus squamatus*	1	—	22·8	—	77	1	0	1	—	18·8	—	74	1	—	5
84.	*Pycnonotus cyaniventris*	2	—	21·9, 24·0	—	73, 77	2	0	0	—	—	—	—	—	—	—
86.	*Pycnonotus simplex*	1	—	22·4	—	89	1	1	2	—	25·7, 27·2	—	85, 90	2	—	8, 8
87.	*Pycnonotus erythropthalmos*	2	—	16·5, 18·8	—	72, 75	2	2	0	—	—	—	—	—	—	—
88.	*Criniger bres*	1	—	29·2	—	96	1	0	4	36·0	34·0–39·4	97·5	91–102	3	7·7	6–9
89.	*Criniger ochraceus*	7	39·6	36·7–46·5	104·9	101–110	7	3	5	43·4	39·6–46·9	110·8	109–114	5	8·8	5–10
90.	*Criniger phaeocephalus*	4	27·0	23·6–31·1	88·0	87–89	4	1	6	29·8	24·6–32·7	98·3	93–105	6	6·1	5–8
91.	*Criniger finschii*	1	—	24·4	—	83	1	0	1	—	25·0	—	86	1	—	8
92.	*Hypsipetes criniger*	5	12·3	11·7–12·9	72·2	71–75	5	0	6	15·1	13·3–18·0	79·0	74–82	6	6·0	4–9
93.	*Hypsipetes charlottae*	0	—	—	—	—	—	—	1	—	25·6	—	87	1	—	8
94.	*Hypsipetes macclellandi*	5	32·7	30·0–37·5	96·4	91–102	5	1	7	33·0	27·6–39·9	100·4	95–112	7	8·9	6–11
95.	*Hypsipetes viridescens*	1	—	36·7	—	101	1	0	0	—	—	—	—	—	—	—
96.	*Hypsipetes flavala*	1	—	27·2	—	92	1	1	2	—	34·3, 35·2	—	102, 101	2	—	11, 7
97.	*Dicrurus remifer*	5	39·9	35·5–44·4	129·8	126–135	5	2	5	44·0	38·8–49·0	135·6	131–139	5	11·6	9–15
98.	*Dicrurus paradiseus*	2	—	63·4, 73·5	—	137, 143	2	0	1	—	70·8	—	145	1	—	16·5
102.	*Platylophus galericulatus*	1	—	77·9	—	127	1	0	0	—	—	—	—	—	—	—
103.	*Corvus enca*	0	—	—	—	—	—	—	1	—	508·5	—	335	1	—	9
104.	*Melanochlora sultanea*	0	—	—	—	—	—	—	2	—	36·1, 41·0	—	101, 108	2	—	8, 11
107.	*Pellorneum capistratum*	2	—	26·4–27·6	—	70, 66	2	1	3	28·4	27·5–29·6	68·7	65–71	3	5·3	4–7
108.	*Trichastoma malaccense*	4	19·1	17·5–20·1	68·3	66–71	5	1	4	21·0	19·4–22·4	71·2	68–74	4	5·1	4·5–6
109.	*Trichastoma sepiarium*	1	—	23·4	—	70	—	—	1	—	21·5	—	75	1	—	6
110.	*Trichastoma bicolor*	2	—	19·3, 19·5	—	78, 85	2	0	2	—	22·0, 26·3	—	89, 87	2	—	4, 5
111.	*Malacopteron magnum*	3	24·3	23·8–24·5	84·0	82–85	2	0	5	25·9	24·1–27·7	90·8	85–96	4	4·0	2–5
112.	*Malacepteron cinereum*	3	15·1	12·7–17·0	73·3	70–76	3	0	4	17·3	15·3–18·4	79·3	77–83	4	7·0	5–8
113.	*Malacopteron magnirostre*	4	18·0	16·8–19·0	76·0	75–77	4	0	4	21·2	19·5–24·9	80·3	77–85	4	7·5	5–10
114.	*Malacopteron affine*	1	—	18·6	—	73	1	1	1	—	15·7	—	76	1	—	4
115.	*Pomatorhinus montanus*	1	—	26·8	—	86	1	0	0	—	—	—	—	—	—	—
116.	*Pomatorhinus hypoleucos*	1	—	69·0	—	100	1	0	2	—	70·4, 74·4	—	109, 105	2	—	6, 8
118.	*Napothera macrodactyla*	0	—	—	—	—	—	—	1	—	48·7	—	91	1	—	3
120.	*Napothera brevicaudata*	3	18·0	17·3–19·0	62·7	60–65	3	1	3	19·8	18·2–21·4	63·3	62–65	3	4·0	4
124.	*Macronus ptilosus*	0	—	—	—	—	—	—	1	—	17·0	—	70	1	—	3
125.	*Stachyris nigriceps*	2	—	16·2, —	—	57, 60	2	1	4	15·1	13·8–16·2	62·5	61–64	4	8·5	7–10
126.	*Stachyris poliocephala*	6	22·2	20·1–25·7	67·3	65–72	6	2	3	24·5	23·3–25·9	68·3	67–69	3	3·3	2–4
127.	*Stachyris nigricollis*	0	—	—	—	—	—	—	2	—	25·5, —	—	69, 71	2	—	4, 10
128.	*Stachyris leucotis*	3	23·3	22·8–23·8	66·0	66 (all)	3	1	3	24·1	21·5–26·5	68·7	66–71	3	4·0	2–5
129.	*Stachyris maculata*	3	24·8	23·6–25·8	81·3	79–84	3	0	5	26·8	24·5–29·6	83·6	80–86	5	5·7	4–7·5

Appendix I (contd.)

		FEMALES							MALES							
Species No.	Species	No.	Weights (g)		Wing (mm)		Reproductive condition		No.	Weights (g)		Wing (mm)		Testis length (mm)		
			Mean	Range	Mean	Range	No. ex'd	No. in breeding cond'n		Mean	Range	Mean	Range	No.	Mean	Range
130.	*Stachyris erythroptera*	4	11·6	11·0–12·2	60·0	59–62	4	0	2	—	13·8, 15·1	—	64, 64	2	—	3, 2
131.	*Stachyris chrysea*	1	—	6·3	—	51	1	0	1	—	7·8	—	53	1	—	7
133.	*Garrulax mitratus*	2	—	57·7, 65·2	—	105, 107	2	1	2	67·4	66·5, 68·2	—	107, 113	2	—	9, 14
134.	*Garrulax erythrocephalus*	3	66·3	58·5–72·0	100·7	97–105	3	1	2	—	59·9, 62·8	—	99, 100	2	—	4, 6
135.	*Cutia nipalensis*	1	—	51·3	—	93	1	0	1	—	62·5	—	93	1	—	15
138.	*Alcippe castaneceps*	7	14·4	12·4–17·1	62·8	61–64	7	1	7	13·2	12·4–13·9	64·4	61–68	7	9·1	8–11
139.	*Alcippe peracensis*	7	—	15·5, 15·8	63·1	60–66	8	1	7	14·3	13·1–16·4	65·4	62–68	6	5·4	2–7
140.	*Alcippe brunneicauda*	5	14·4	13·5–15·0	68·4	65–71	5	0	5	14·1	13·3–15·3	71·6	70–72	5	3·3	1–5
141.	*Minla strigula*	1	—	19·6	—	67	1	1	4	19·5	18·7–20·2	66·8	64–69	4	6·5	6–7
143.	*Heterophasia picaoides*	1	—	43·3	—	113	1	0	2	—	40·9, 41·7	—	117, 122	2	—	14, 16
145.	*Copsychus pyrropyga*	1	—	34·5	—	98	1	0	2	—	37·8, 40·1	—	101, 89	2	—	9, 9
146.	*Copsychus malabaricus*	2	—	29·5, 30·5	—	88, 84	2	0	2	—	31·0, 35·8	—	94, 98	2	—	6, 8·5
147.	*Enicurus leschenaulti*	1	—	24·8	—	88	1	0	1	—	34·0	—	93	1	—	2
148.	*Enicurus ruficapillus*	2	—	24·8, 29·9	—	87, 87	2	0	3	29·1	27·9–30·0	92·0	91–93	3	3·3	3–4
152.	*Phylloscopus trivirgatus*	0	—	—	—	—	—	—	3	7·9	7·0–9·3	56·3	55–59	3	4·5	2·5–8
154.	*Seicercus montis*	1	—	5·8	—	56	1	0	1	—	6·5	—	52	1	—	5
155.	*Orthotomus cuculatus*	1	—	5·6	—	42	1	1	1	—	5·6	—	45	1	—	5·5
158.	*Rhipidura albicollis*	7	10·5	9·4–11·7	78·0	76–84	7	0	4	12·8	10·5–14·7	84·5	81–87	4	8·0	8–9
159.	*Rhipidura perlata*	1	—	12·1	—	83	1	0	1	—	12·0	—	91	1	—	7
160.	*Culicicapa ceylonensis*	0	—	—	—	—	—	—	4	7·7	7·0–8·6	61·3	59–63	4	4·0	3–5
164.	*Muscicapa grandis*	2	—	29·0, 34·9	—	99, 94	2	0	9	30·0	27·5–34·9	99·6	97–102	8	8·3	6–10
166.	*Muscicapa hyperythra*	2	—	8·0, 9·6	—	55, 61	3	2	10	7·6	6·3–8·8	60·4	56–66	10	5·8	4–8
167.	*Muscicapa dumetoria*	1	—	8·2	—	55	1	0	2	—	8.5, 9.1	—	62, 60	2	—	4, 3
169.	*Muscicapa westermanni*	0	—	—	—	—	—	—	1	—	—	—	60	1	—	3
172.	*Rhinomyias umbratilis*	2	—	13·8, 14·4	—	72, 73	2	0	2	—	17·8, 16·2	—	76, 78	2	—	2, 6
173.	*Philentoma pyrhoptera*	1	—	16·2	—	80	1	0	4	16·4	14·7–17·6	80·2	77–83	4	6·2	4–8
174.	*Philentoma velata*	3	23·6	22·9–24·2	93·3	89–96	3	0	1	—	26·6	—	100	1	0	6
175.	*Hypothymis azurea*	1	—	11·0	—	68	1	0	2	—	7·3–11·7	—	70, 70	2	—	8, 3
176.	*Terpsiphone paradisi*	1	—	16·3	—	87	1	1	3	18·6	18·1–19·2	96·3	95–98	2	—	9, 10
177.	*Anthreptes simplex*	0	—	—	—	—	—	—	1	—	9·2	—	63	1	—	5
179.	*Hypogramma hypogrammicum*	3	11·1	9·7–12·8	62·7	60–64	3	1	9	10·4	7·8–12·3	65·5	61–70	6	4·9	4–6
182.	*Arachnothera longirostris*	5	12·2	10·8–14·0	61·2	59–63	6	2	7	14·0	12·9–15·6	68·1	65–71	7	6·4	1·5–9
184.	*Arachnothera affinis*	1	—	20·6	—	76	2	0	4	22·6	20·5–24·9	85·5	83–88	4	5·5	3·5–7
185.	*Arachnothera magna*	1	—	23·9	—	90	1	0	4	31·5	30·0–34·5	92·8	89–96	4	6·8	6–8
189.	*Prionochilus maculatus*	2	—	7·8, 7·9	—	52, 54	2	0	3	9·1	7·7–11·8	53·7	51–56	3	4·9	3–6
191.	*Pyrrhula nipalensis*	2	—	19·8, 21·4	—	79, 82	2	0	2	—	18·6, 22·2	—	82, 84	2	—	3, 1·5

MOULT RECORDS

Moult was occurring only among species listed; figures give number in moult (with number examined in parentheses). Primaries numbered centrifugally, secondaries centripetally.

Species No.	
37. **Merops viridis* 1 (1):	female, 23 February 1967, moulting from juvenile to adult plumage.
63. *Calyptomena viridis* 2 (7):	male, 19 February 1967, moulting from juvenile to adult plumage; adult female, 7 April 1967, heavy moult with renewal in humerals and rectrices.
64. *Cymbirhynchus macrorhynchos* 1 (1):	male, 20 February 1967, moulting from juvenile to adult plumage.
76. **Delichon dasypus* 1 (1):	not sexed, 15 February 1968, heavy moult, with primary VII, secondary III growing.
90. *Criniger phaeocephalus* 1 (18):	adult female, reproductively inactive, 12 February 1967, moult in secondaries.
100. *Oriolus xanthonotus* 1 (1):	male, 14 April 1967, moulting from juvenile to adult plumage.
128. *Stachyris leucotis* 2 (6):	male and female, 27 February, with asymmetrical moult in inner primaries, secondaries and humerals.
130. *Stachyris erythroptera* 1 (9):	adult, 8 April 1967, renewing primary III and secondary I.
138. *Alcippe castaneceps* 1 (35):	adult, 25 March 1967, limited body moult only.
148. *Enicurus ruficapillus* 1 (6):	male, 18 February 1967, heavy moult with primary IV and secondary I growing.
191. *Pyrrhula nipalensis* 5 (6):	4 adults, 1 subadult, in advanced moult with replacement of the primaries complete or nearly so.

*Palaearctic migrants or non-breeding visitors.

FURTHER BREEDING RECORDS

Species No.	
5. *Microhierax fringillarius*:	A pair at a hole, apparently nesting, seen repeatedly in February 1967.
12. *Macropygia ruficeps*:	A typical columbiform nest, with one broken white egg on the ground below, found at 6650 ft, 10 April 1967.
65. *Eurylaimus javanicus*:	A pair built at least two nests high in the tualang tree overhanging Base camp in February–March 1967; successful breeding was not confirmed. Juveniles, a male and a female, collected on 8 April 1967.
107. *Pellorneum capistratum*:	Juvenile netted on 10 February 1967.
112. *Malacopteron cinereum*:	Juveniles netted on 10, 16, 17 and 21 February 1967.
113. *Malacopteron magnirostre*:	A juvenile netted on 20 February 1967.
117. *Napothera epilepidota*:	Nesting February 1968.
130. *Stachyris erythroptera*:	Juvenile netted on 9 April 1967.
134. *Garrulax erythrocephalus*:	Adult with two newly fledged young seen on 26 March 1967.
140. *Alcippe brunneicauda*:	Juvenile netted on 8 April 1967.
145. *Copsychus pyrropyga*:	Juvenile netted on 8 April 1967.
148. *Enicurus ruficapillus*:	Juvenile netted on 14 February 1967.
182. *Arachnothera longirostris*:	Juvenile netted on 11 April 1967.
191. *Pyrrhula nipalensis*:	Juveniles, male and female, collected 26 March 1967.

APPENDIX 2

Breeding condition among female mammals on Gunong Benom, 11 February–15 April 1967. Observations are based on specimens autopsied.

Species		Number of females			Number of foetuses		
No.	Species	Examined	Lactating	Pregnant	Mean	Range	Notes
3.	*Cynocephalus variegatus*	1	0	1	1	—	*
4.	*Cynopterus brachyotis*	1	0	1	1	—	*
6.	*Balionycteris maculata*	1	0	1	1	—	*
7.	*Chironax melanocephalus*	3	0	1	1	—	
8.	*Megaerops ecaudatus*	2	0	2	1	1	
9.	*Macroglossus minimus*	1	0	0	—	—	
12.	*Rhinolophus affinis*	7	1	4	1	1	*
13.	*Rhinolophus stheno*	6	0	5	1	1	*
14.	*Rhinolophus refulgens*	9	0	9	1	1	*
15.	*Rhinolophus macrotis*	1	0	1	1	—	*
16.	*Rhinolophus trifoliatus*	3	0	3	1	1	
18.	*Hipposideros galeritus*	1	1	0	—	—	*
19.	*Hipposideros diadema*	1	0	1	1	—	*
22.	*Murina cyclotis*	1	0	1	2	—	*
30.	*Presbytis obscura*	2	0	1	1	—	*
37.	*Ratufa bicolor*	1	0	1	1	—	*
38.	*Ratufa affinis*	1	0	0	—	—	
39.	*Calosciurus notatus*	1	0	0	—	—	
41.	*Callosciurus flavimanus*	4	0	1	1	—	*
42.	*Callosciurus nigrovittatus*	4	0	1	2	—	*
44.	*Sundasciurus tenuis*	2	1	0	—	—	*
45.	*Sundasciurus lowii*	1	0	0	—	—	
46.	*Tamiops macclellandii*	1	0	1	3	—	
47.	*Lariscus insignis*	2	0	0	—	—	
48.	*Rhinosciurus laticaudatus*	1	0	0	—	—	
49.	*Iomys horsfieldii*	1	0	1	3	—	*
51.	*Petaurista petaurista*	3	0	2	1	—	*
53.	*Rattus tiomanicus*	1	0	0	—	—	
54.	*Rattus muelleri*	2	0	0	—	—	
55.	*Rattus bowersii*	2	0	0	—	—	
56.	*Rattus cremoriventer*	1	1	0	—	—	*
58.	*Rattus rajah*	2	0	0	—	—	
59.	*Rattus inas*	5	2	2	3, 4	—	*
60.	*Rattus whiteheadi*	4	2	1	3	—	*
61.	*Rattus sabanus*	18	5	1	2	—	*
62.	*Rattus edwardsi*	5	4	0	—	—	
67.	*Arctogalidia trivirgata*	1	0	0	—	—	
73.	*Tragulus javanicus*	1	0	1	1	—	

Notes to Appendix 2

3. 5 March; foetus in left uterine horn, weight 24·5 g.
4. 20 February; foetus in left uterine horn.
6. 25 February; foetus in left uterine horn.
12. All implantations in right uterine horn; all pregnancies in February, lactating on 11 March.
13. All specimens 9–25 February; all implantations in right uterine horn.

14. All specimens 12–25 February; all implantations in right uterine horn.
15. 23 February; implantation site not noted.
16. 10–21 February; implantation noted for one specimen only; in right horn.
18. 8 March.
19. 11 February.
22. 20 February.
30. Both dated 3 March; one with advanced foetus, the other with a ripe graafian follide in the left ovary.
37. 10 April; implanted in right uterus.
41. The single pregnancy on 18 March; implanted in right uterus.
42. Pregnancy on 9 March.
44. Lactating on 10 April.
46. 2 April; all foetuses in left uterus.
49. 7 March; 2 foetuses in left uterus, 1 in right.
51. Pregnancies on 16 and 23 February; both implanted in right uterus.
56. Lactating on 10 March.
59. 23 March, lactating, not pregnant; 10 April, gave birth to 3 young in the trap; lactating and also pregnant, presumably as a consequence of post-partum oestrus with 4 embryos all in the right uterus.
60. Pregnant on 1 March, all foetuses in the right uterus; lactating and not pregnant on 8, 14 March.
61. Pregnancy on 24 February, both foetuses in right uterus.
73. 23 February.

TABLE I

ALTITUDINAL RECORDS OF FOREST BIRDS ON GUNONG BENOM

Records for each species within the observed limits of its altitudinal range are given by symbols representing 100 ft intervals: n = netted, x = collected by other means, s = sight record or vocalisation, - = presence inferred.

Species No.	Altitude ('000 ft)	1 2 3 4 5 6
1.	*Ictinaetus malayensis*	x
2.	**Hieraaetus kienerii*	x-s
3.	*Spilornis cheela*	s--------s----------------s-s
4.	*Spizaetus alboniger*	s
5.	*Microhierax fringillarius*	s------s
6.	*Polyplectron inopinatum*	x
7.	*Argusianus argus*	ss------s-xs-------s--s
8.	*Rollulus rouloul*	x
9.	*Rhizothera longirostris*	s-----------------------s-s
10.	*Ducula badia*	ss-------------s-ss------x
11.	*Treron curvirostra*	x
12.	*Macropygia ruficeps*	s-s---x---x----------------------s-------s---------sx-----x
13.	*Chalcophaps indica*	nn
14.	*Loriculus galgulus*	s-s-------s------ss------s
15.	*Cuculus micropterus*	s-----s---s-------s
16.	*Cuculus sparverioides*	s-s--------s-------s
17.	*Chrysococcyx xanthorhynchus*	s------s
18.	*Surniculus lugubris*	n--------s
19.	*Phaenicophaeus diardi*	x
20.	*Phaenicophaeus curvirostris*	x---------s

Table 1 (contd).

Species No.	Altitude ('000 ft)	1	2	3	4	5	6
21.	*Phaenicophaeus chlorophaeus*	sx--x-----	--------s				
22.	*Phaenicophaeus javanicus*	x--------	-n-s-----s				
23.	*Otus rufescens*	n--------	-----------	-----------	------------	-n	
24.	*Otus spilocephalus*			s--	-----------	-n----------n	
25.	*Otus bakkamoena*	n--------	--s				
26.	*Glaucidium brodiei*			s--	------s-----	-------------n	
27.	*Phodilus badius*	n					
28.	*Chaetura leucopygialis*	s--------	ss				
29.	*Hemiprocne comata*	x--------	-s				
30.	*Harpactes diardii*	s-----	---s-----n				
31.	*Harpactes oreskios*		s				
32.	*Harpactes duvaucelii*	x------x--	---------n				
33.	*Harpactes erythrocephalus*			n---	---s		
34.	**Ceyx erithacus*	n					
35.	*Ceyx rufidorsus*	n					
36.	*Halcyon concreta*	n--------	---------n				
37.	**Merops viridis*	x--s-----s--	-----s				
38.	*Nyctiornis amicta*		s-------n-s				
39.	*Berenecornis comatus*	s					
40.	*Rhyticeros undulatus*	s-----s---	-----------	------ss---	s		
41.	*Anorhinus galeritus*	sx--------	-s------s---	-------s			
42.	*Buceros rhinoceros*	s---s--s--	-s------s-s				
43.	*Rhinoplax vigil*	s----s----	--------ss	-----s--s			
44.	*Psilopogon pyrolophus*			sx-x	-----x-----	x-s--------s	
45.	*Megalaima chrysopogon*	s-----x---	--------x--	s------s			

Table 1 (contd.)

Species No.	Altitude ('000 ft)	1	2	3	4	5	6
46.	*Megalaima mystacophanos*	s-s-----ss					
47.	*Megalaima franklinii*				x-s-----s-------s		
48.	*Megalaima oorti*		s-----s----xx--s				
49.	*Megalaima henricii*	x-----x-----------s					
50.	*Megalaima australis*	s-----x-----------s-s					
51.	*Calorhamphus fuliginosus*	x-s-----s-------s					
52.	*Indicator archipelagicus*	x					
53.	*Sasia abnormis*	n----------------n					
54.	*Picus puniceus*	s----s--x					
55.	*Picus chlorolophus*				s-s-s-------x		
56.	*Picus mentalis*			x			
57.	*Meiglyptes tukki*	n--------------------------n					
58.	*Meiglyptes tristis*		s				
59.	*Blythipicus pyrrhotis*					s	
60.	*Blythipicus rubiginosus*	s---------x------s--------s					
61.	*Chrysocolaptes validus*	x--x----------s					
62.	*Hemicercus concretus*	s					
63.	*Calyptomena viridis*	n---------n-------n					
64.	*Cymbirhynchus macrorhynchos*	x					
65.	*Eurylaimus ochromalus*	x--s-----s-------s					
66.	*Eurylaimus javanicus*	sx----x--s					
67.	*Pitta caerulea*	x					
68.	**Pitta sordida*	x					
69.	*Coracina fimbriata*		s				
70.	*Coracina novaehollandiae*			x-x-----------------x			

Table 1 (contd.)

Species No.	Altitude ('000 ft)	1	2	3	4	5	6
71.	*Hemipus hirundinaceus*	s					
72.	*Hemipus picatus*		s				
73.	*Pericrocotus solaris*			s-sx-	---------s-	-s-ss--s---	x-------
74.	*Pericrocotus cinnamomeus*	s---------	s				
75.	*Pericrocotus flammeus*	x-s-------	s				
76.	*Delichon dasypus*		x				
77.	*Aegithina lafresneyi*	s					
78.	*Chloropsis cyanopogon*	x-s-------	n				
79.	*Chloropsis sonnerati*	s					
80.	*Chloropsis cochinchinensis*	s-s----xs-	sx-----ss-	------s-s			
81.	*Chloropsis hardwickii*				s-----	s	
82.	*Irena puella*	x--x----s	ss				
83.	*Pycnonotus squamatus*	xx----s					
84.	*Pycnonotus cyaniventris*	sx--------	-n				
85.	*Pycnonotus brunneus*	s------s					
86.	*Pycnonotus simplex*	x---------	s------s				
87.	*Pycnonotus erythrophthalmos*	x---------	xn------x				
88.	*Criniger bres*	n---------	xn				
89.	*Criniger ochraceus*		n-	---------n			
90.	*Criniger phaeocephalus*	n---------	n--------n				
91.	*Criniger finschi*	x----x					
92.	*Hypsipetes criniger*	n------s-s	n--------n				
93.	*Hypsipetes charlottae*	x-s	s				
94.	*Hypsipetes macclellandii*			sx--	---ss------	x-----x---x	------s
95.	*Hypsipetes viridescens*	x-ss	s------s				

Table 1 (contd.)

Species No.	Altitude ('000 ft)	1 2 3 4 5 6
96.	*Hypsipetes flavala*	ss-n-----s-----------n
97.	*Dicrurus remifer*	ss---------s-------n-------------sn--s--s-n-n
98.	*Dicrurus paradiseus*	n
99.	*Dicrurus annectans*	s----ss-x
100.	*Oriolus xanthonotus*	xx
101.	*Oriolus cruentus*	s-------s-s
102.	*Platylophus galericulatus*	s-------------------n
103.	*Corvus enca*	x--------s
104.	*Malanochlora sultanea*	s--s-------------s----------x---s
105.	*Sitta frontalis*	s------s
106.	*Sitta azurea*	s
107.	*Pellorneum capistratum*	n
108.	*Trichastoma malaccense*	n---------n-------nn
109.	*Trichastoma sepiarium*	n
110.	*Trichastoma bicolor*	n
111.	*Malacopteron magnum*	n---------n
112.	*Malacopteron cinereum*	n---------n--------n
113.	*Malacopteron magnirostre*	n---------n-----ss-n
114.	*Malacopteron affine*	n
115.	*Pomatorhinus montanus*	s-s----s-n
116.	*Pomatorhinus hypoleucos*	n-s-s------------s------n-----s
117.	*Napothera epilepidota*	s---------s
118.	*Napothera macrodactyla*	n
119.	*Napothera loricata*	n
120.	*Napothera brevicaudata*	sn-------------n-------n-n

Table 1 (contd.)

Species No.	Altitude ('000 ft)	1	2	3	4	5	6
121.	*Kenopia striata*	x					
122.	*Microura pusilla*			s--------------s-s-------s			
123.	*Macronus gularis*	s-------s--------s					
124.	*Macronus ptilosus*	n					
125.	*Stachyris nigriceps*	n------------------n----------sn					
126.	*Stachyris poliocephala*	n----------n					
127.	*Stachyris nigricollis*		n				
128.	*Stachyris leucotis*	n----------n-------sn					
129.	*Stachyris maculata*	n----------n					
130.	*Stachyris erythroptera*	n----------n----s---n					
131.	*Stachyris chrysea*			ss-----s-------sn--s--s-n-n			
132.	*Garrulax lugubris*			x-----s			
133.	*Garrulax mitratus*			x-------------sn---x			
134.	*Garrulax erythrocephalus*				x----sn--s-------n-----s		
135.	*Cutia nipalensis*				sn----------x---s		
136.	*Pteruthius melanotis*				s---s------x		
137.	*Pteruthius flaviscapis*			sx-s---s----------ss			
138.	*Alcippe castaneceps*			n--------------n--s------n			
139.	*Alcippe peracensis*		n-------ssn--------s-----n--s--s---n				
140.	*Alcippe brunneicauda*	n-s-------sn-------s-n					
141.	*Minla strigula*					ss------n----x-xs	
142.	*Yuhina zantholeuca*		ss-----ss-----------s				
143.	*Heterophasia picaoides*		s		---x-------x--x----s		
144.	*Erithacus cyane	n---------nn---------n					
145.	*Copsychus pyrropyga*		n------s-n				

Table 1 (contd.)

Species No.	Altitude ('000 ft)	1	2	3	4	5	6
146.	*Copsychus malabaricus*	n-----s-s-	n				
147.	*Enicrurus leschenaulti*	n					
148.	*Enicrurus ruficapillus*	n---------	n				
149.	*Gerygone fusca*	s--s--s---	s------s--	-----s			
150.	**Phylloscopus coronatus*	s---------	s---------	-----------	---s		
151.	**Phylloscopus borealis*		--s--				
152.	*Phylloscopus trivirgatus*					sn-n	
153.	*Seicercus castaniceps*			ss			
154.	*Seicercus montis*					s--s-n-n	
155.	*Orthotomus cuculatus*				s-s----	-n-ss------n	-------s
156.	*Orthotomus sericeus*	s					
157.	*Orthotomus atrogularis*	s-sss					
158.	*Rhipidura albicollis*			s-n--	-----s----	ss-----s-n-n	---s---s
159.	*Rhipidura perlata*	n--------	sn-s----sn				
160.	*Culicicapa ceylonensis*	n---------	s---------	-------sn--	---s		
161.	**Muscicapa latirostris*	s------	----s---s				
162.	**Muscicapa sibirica*		s				
163.	**Muscicapa ferruginea*		s				
164.	*Muscicapa grandis*				s---	------n-s--	-s---n
165.	**Muscicapa rubeculoides*	n--------	sn				
166.	*Muscicapa hyperythra*				s-	nn-------s-n	------s
167.	*Muscicapa dumetoria*	n					
168.	*Muscicapa unicolor*	s					
169.	*Muscicapa westermanni*				s---x-----s	-----------n	
170.	*Muscicapa solitaris*			n			

Table 1 (contd.)

Species No.	Altitude ('000 ft)	1	2	3	4	5	6
171.	*Muscicapa hodgsoni*			sn-----s-----------------s-s			
172.	*Rhinomyias umbratilis*	s--n------s-n					
173.	*Philentoma pyrhoptera*	n----------n---------n					
174.	*Philentoma velatum*	n-----x---n---------n					
175.	*Hypothymis azurea*	n-------s-----------n					
176.	*Terpsiphone paradisi*	x-----------n					
177.	*Anthreptes simplex*		n				
178.	*Anthreptes singalensis*		s				
179.	*Hypogramma hypogrammicum*	n----------n---------n-----------s					
180.	*Aethopyga saturata*			ss-------------ss--s------s------s			
181.	*Aethopyga mystacalis*	s					
182.	*Arachnothera longirostris*	n-----s---n---------n----------n					
183.	*Arachnothera robusta*	s					
184.	*Arachnothera affinis*	n-s---s-s-n					
185.	*Arachnothera magna*			n----------n-sn			
186.	*Dicaeum ignipectus*			ss--------------------s			
187.	*Dicaeum trigonostigma*	s					
188.	*Dicaeum agile*				s		
189.	*Prionochilus maculatus*	n-------s-n---------n--------s					
190.	*Zosterops everetti*	ss-s----------------s					
191.	*Pyrrhula nipalensis*					n-----s---sx	

* Migrant or non-breeding visitor.

TABLE 2

SUMMARY OF MIST-NETTING CATCHES OF BIRDS

Camp	Base	2	2½	3	4	5
Altitude (ft)	700–900	1600–1700	2500–2600	3500–3600	4700–5000	5800–6000
Net/days	166	104	80	159	90	98
No. species netted	45	34	31	19	16	19
Total birds netted	266	114	79	76	60	81
Birds/net/day	1·6	1·1	1·0	0·5	0·7	0·8
Mean birds/species	5·9	3·4	2·5	4·0	3·8	4·3
Arachnothera longirostris	96	17	11	4	0	0
Alcippe brunneicauda	4	8	4	0	0	0
Alcippe peracensis	0	0	1	28	6	8
Alcippe castaneceps	0	0	0	2	11	22

TABLE 3

MAMMALS CAUGHT IN CAGE-TYPE TRAPS ON GUNONG BENOM, 1967

Altitude range (ft)	< 1000	1–1900	2–2900	3–3900	4–4900	5–5900	> 6000	Total
Trap-nights	3380	1716	155	200	122	104	100	5777
Echinosorex gymnurus	1						—	1
Tupaia minor	1				—	—	—	1
Callosciurus notatus	6		—	—	—	—	—	6
Callosciurus caniceps	1	—	—	—	—	—	—	1
Callosciurus nigrovittatus	5	—	—	—	—	—	—	5
Sundasciurus tenuis	1	—	—	—	—	—	—	1
Sundasciurus lowii	1	1	—	—	—	—	—	2
Lariscus insignis	2	1	—	—	—	—	—	3
Rhinosciurus laticaudatus	4		—	—	—	—	—	4
Iomys horsfieldii	4		—	—	—	—	—	4
Rattus tiomanicus	—	—	—	1	—	—	—	1
Rattus muelleri	6	—	—	—		—	—	6
Rattus bowersii	3	—	—		—	—	—	3
Rattus cremoriventer	3	—	—	—	—	—	—	3
Rattus surifer	—	—	1	—	—	—	—	1
Rattus rajah	4	6	1	—	—	—	—	11
Rattus inas	—		—	1	1	2	5	9
Rattus whiteheadi	3	1	1	—			—	5
Rattus sabanus	32	4	1	—		—	—	37
Rattus edwardsi	—	—	—	2	4	2	3	11
Total	77	13	4	4	5	4	8	115
Catch/100 trap nights	2·3	0·76	2·6	2·0	4·1	3·8	8	2·0
Total species	16	5	4	3	2	2	2	20

TABLE 4

ALTITUDINAL RECORDS OF FOREST MAMMALS ON GUNONG BENOM

Records for each species within the observed limits of its altitudinal range are given by symbols representing 100 ft intervals: x = specimen collected, s = sight record, t = tracks or other traces, * = material in carnivore dung, - = presence inferred.

Species No.	Altitude ('ooo ft)	1	2	3	4	5	6
1.	*Echinosorex gymnurus*	x					
2.	*Crocidura fuliginosa* (?)					s	
3.	*Cynocephalus variegatus*	xx					
4.	*Cynopterus brachyotis*	x----------	x				
5.	*Penthetor lucasi*			x			
6.	*Balionycteris maculata*	x---------	x				
7.	*Chironax melanocephalus*	x------	----------	---x----	-------xx-	x	
8.	*Aethalops alecto*						x
9.	*Megaerops ecaudatus*	x					
10.	*Macroglossus minimus*	xx					
11.	*Emballonura monticola*	s------x					
12.	*Rhinolophus affinis*	x-x-------	xx------x				
13.	*Rhinolophus stheno*	x-x-------	xx------x	---------x			
14.	*Rhinolophus refulgens*	xxx-------	xx--------	--------x			
15.	*Rhinolophus macrotis*	x---------	-------x	---------x			
16.	*Rhinolophus trifoliatus*	x					
17.	*Hipposideros bicolor*	x					
18.	*Hipposideros galeritus*	x					
19.	*Hipposideros diadema*	x					
02.	*Pipistrellus javanicus*		x				

Table 4 (contd.)

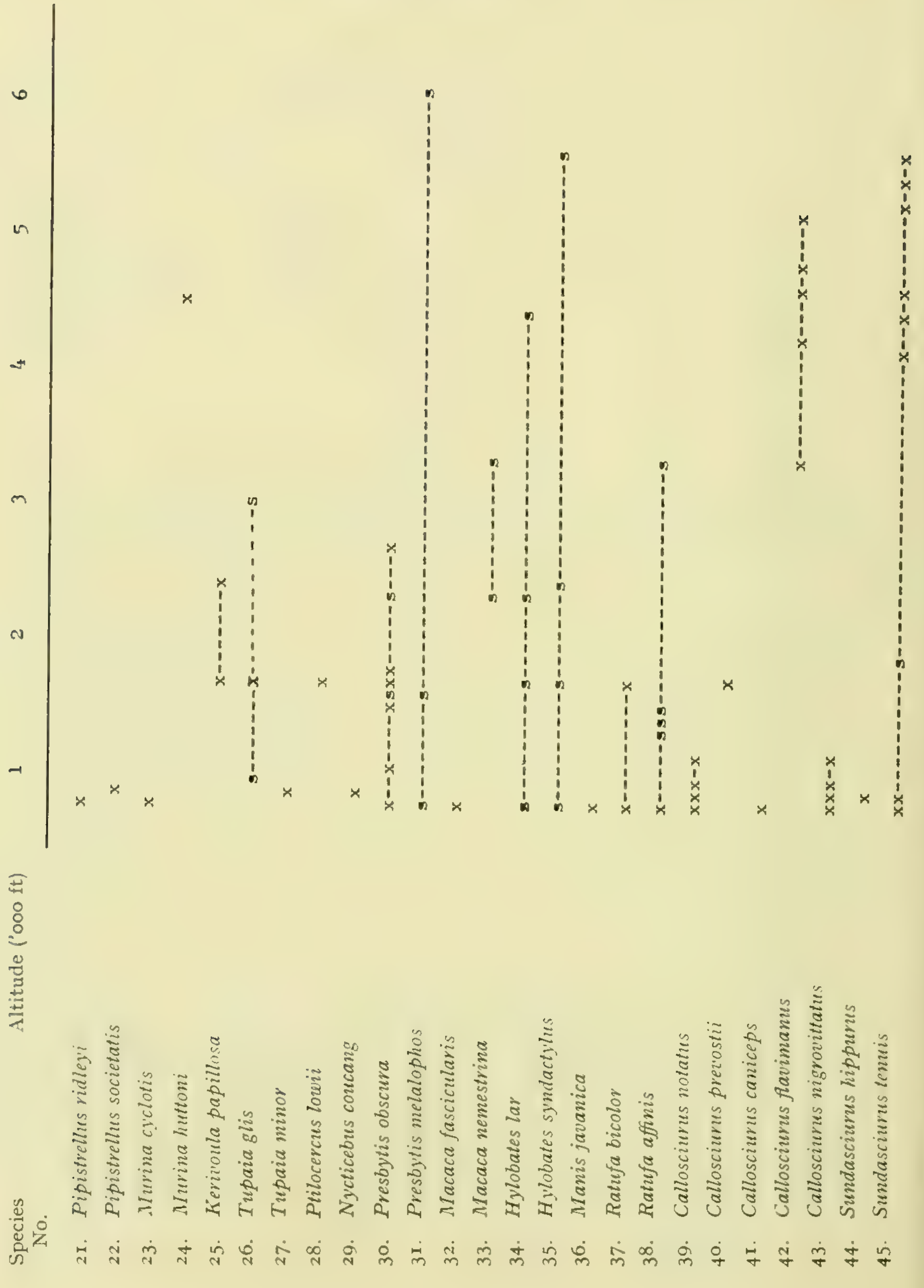

Table 4 (contd.)

Species No.	Altitude ('000 ft)	1	2	3	4	5	6
46.	*Sundasciurus lowii*	x---x					
47.	*Tamiops macclellandii*			x-	-------x---	xx--------	-x
48.	*Lariscus insignis*	xxxx-x					
49.	*Rhinosciurus laticaudatus*	xx					
50.	*Hylopetes spadiceus*		x				
51.	*Iomys horsfieldii*	x-------	-----------	-----------	----------	--x	
52.	*Pteromyscus pulverulentus*		x				
53.	*Aeromys tephromelas*	x--------	---------x				
54.	*Petaurista petaurista*	xxx----xx					
55.	*Petaurista elegans*	xx					
56.	*Chiropodomys gliroides*	s---------	x				
57.	*Rattus tiomanicus*			x			
58.	*Rattus muelleri*	xx					
59.	*Rattus bowersii*	x					
60.	*Rattus cremoriventer*	xx					
61.	*Rattus surifer*		x				
62.	*Rattus rajah*	xx---x---	-x-------x				
63.	*Rattus inas*			x--	-----------	x---------	x-x
64.	*Rattus whiteheadi*	x-x-----	---------x				
65.	*Rattus sabanus*	xxx-xx--x	-x--------	---x			
66.	*Rattus edwardsi*			xx-	--x-------x	-x---------	x
67.	*Atherurus macrourus*		*				
68.	*Helarctos malayanus*	t-------t	s------				
69.	*Prionodon linsang*			x			
70.	*Arctictis binturong*	x					

Table 4 (contd.)

Species No.		Altitude ('ooo ft) 1 2 3 4 5 6
71.	*Arctogalidia trivirgata*	x--s
72.	*Hemigalus derbyanus*	x
73.	*Panthera tigris*	t
74.	*Panthera pardus*	t
75.	*Felis bengalensis*	sx
76.	*Elephas maximus*	tt
77.	*Tapirus indicus*	-t------tt-t------t---------------t-t-t-t-t-t-t--t-t-t-t-t-t
78.	*Sus sp.*	t------t--t------t-----------------------------t
79.	*Tragulus javanicus*	x--s
80.	*Muntiacus muntjak*	t
81.	*Capricornis sumatraensis*	s------------------t

TABLE 5

RELATIONS BETWEEN BIRD FAUNAS OF DIFFERENT ALTITUDINAL ZONES. FIGURES GIVE THE TOTAL NUMBER OF SPECIES IN EACH CATEGORY

	Altitude zone ('000 ft)	SPECIES IN COMMON						
		< 1	1–1·9	2–2·9	3–3·9	4–4·9	5–5·9	6–6·9
TOTAL SPECIES	< 1	*109*	80	53	20	4	2	1
	1–1·9	141	*112*	64	24	5	4	3
	2–2·9	126	118	*70*	28	7	4	2
	3–3·9	145	144	99	*56*	31	25	17
	4–4·9	148	130	106	68	*43*	34	27
	5–5·9	146	147	105	80	48	*39*	31
	6–6·9	139	140	99	69	47	39	*31*

TABLE 6

RELATIONS BETWEEN MAMMAL FAUNAS OF DIFFERENT ALTITUDINAL ZONES FIGURES GIVE THE TOTAL NUMBER OF SPECIES IN EACH CATEGORY

	Altitude zone ('000 ft)	SPECIES IN COMMON						
		< 1	1–1·9	2–2·9	3–3·9	4–4·9	5–5·9	6–6·9
TOTAL SPECIES	< 1	*62*	33	22	14	8	8	5
	1–1·9	69	*40*	23	14	9	8	5
	2–2·9	56	42	*25*	15	9	7	5
	3–3·9	70	47	31	*21*	12	11	6
	4–4·9	67	45	30	23	*14*	12	9
	5–5·9	67	45	29	23	15	*13*	9
	6–6·9	67	45	29	23	15	14	10

TABLE 7

SOERENSEN'S COEFFICIENT CALCULATED FOR THE BIRD AND MAMMAL FAUNAS OF SUCCESSIVE 1000-FT ALTITUDINAL ZONES

Altitude zone ('000 ft)	< 1	1–1·9	2–2·9	3–3·9	4–4·9	5–5·9	6–6·9
				BIRDS			
< 1		72	59	24	5·2	2·7	1·4
1–1·9	65		71	29	6·5	5·3	4·2
2–2·9	51	71		44	12	7·3	4·1
3–3·9	34	46	65		63	53	39
4–4·9	21	33	46	69		83	73
5–5·9	21	30	37	65	86		89
6–6·9	14	20	29	39	75	78	
				MAMMALS			

TABLE 8

VALUES OF τ (INCLUDING COMMON 0) FOR BIRD SPECIES LISTS FROM SIX NETTING SITES ON GUNONG BENOM

Camp	Base	2	2½	3	4	5
2	0·44					
2½	0·25	0·35				
3	−0·27	−0·26	−0·10			
4	−0·41	−0·35	−0·30	0·21		
5	−0·42	−0·36	−0·30	0·14	0·56	—

ADDENDUM

In a recent publication, Medway & Wells (1971) have listed the mammals and birds recorded during a survey of 200 ha of forest at 200–250 ft elevation near Kuala Lompat (102°15′E, 3°42′N), in the lowlands flanking the south-eastern slopes of Gunong Benom. The area sampled lies on the true right bank of the Kerau river at its confluence with the Lompat. Base camp of the 1967 expedition was situated in the upper reaches of the same catchment. The fauna of Kuala Lompat can thus be accepted as representative of that formerly occurring at similar elevations below Base camp, on land where the natural vegetation has since been cleared.

Excluding preliminary visits, the survey at Kuala Lompat was limited to five days of continuous observation. This period was too brief to yield an exhaustive list of the mammals present. Comparatively little effort was made to obtain nocturnal forms (including bats, flying squirrels and small carnivores) which were inadequately sampled. With these limitations, the total number of mammal species recorded was 56 (Table *A*). Of those not previously found on Benom itself, the two rats (Harrison, 1957), the common palm civet (Medway, 1969), the sambhur (Kitchener, 1961) and the gaur (Weigum, 1970) normally frequent, or are even restricted to grassland, past or present cultivation, or human habitation—habitats absent at higher elevations on north-east Gunong Benom. Differences in the bat fauna must be attributed in part, at least, to irregularities in sampling.

In contrast to the obviously incomplete list of mammals, the birds were more effectively tallied. In all, 154 species were identified of which 148 (including 11 migrants) were found in forest, the forest edge or the banks of rivers and streams running through the forest. This forest-adapted fauna shows affinity with the lowland community found on north-east Gunong Benom. It included 82 species recorded at 600–1000 ft, and a further 12 observed in 1967–68 at higher altitudes within the lowland range (Table *B*, *cf.* Table 1 above).

It also, however, exhibits an increased diversity with a total of 45 additional species not noted on the slopes of the mountain (Table *B*). Although some of these birds may have been missed by accidents of collection, or otherwise overlooked during the expeditions of 1967–68, many are clearly restricted by their ecology to lowland habitats including the riparian biotope. The Kuala Lompat list thus further emphasizes the altitudinal specializations exhibited by Malayan birds, stressing in particular the great diversity of the avifauna of the extreme lowlands and the existence of patterns of zonation within the first 1000 ft above sea level.

TABLE *A*

Mammals recorded at Kuala Lompat. Species marked * were not found on north-east Gunong Benom

**Cynopterus horsfieldi*
Cynopterus brachyotis
Balionycteris maculata
Penthetor lucasi
Macroglossus minimus
**Eonycteris spelaea*
**Nycteris javanica*
Rhinolophus stheno
Rhinolophus refulgens
Rhinolophus trifoliatus
**Rhinolophus luctus*
**Hipposideros sabanus*
Hipposideros galeritus
**Hipposideros armiger*
Hipposideros diadema
**Myotis mystacinus*
Murina cyclotis
**Murina suilla*
Tupaia glis
Tupaia minor
Presbytis obscura
Presbytis melalophos
Macaca fascicularis
Macaca nemestrina
Hylobates lar
Hylobates syndactylus
Manis javanica
Ratufa bicolor
Ratufa affinis
Callosciurus notatus
Callosciurus caniceps
Callosciurus prevostii
Sundasciurus hippurus
Sundasciurus tenuis
Sundasciurus lowii
Rhinosciurus laticaudatus
Petaurista petaurista
Rattus tiomanicus
**Rattus argentiventer*
**Rattus exulans*
Rattus muelleri
Rattus bowersii
Rattus cremoriventer
Rattus surifer
Rattus rajah
Rattus whiteheadi
Rattus sabanus
**Paradoxurus hermaphroditus*
Elephas maximus
Sus scrofa
Tragulus javanicus
**Tragulus napu*
Muntiacus muntjak
**Cervus unicolor*
**Bos gaurus*

TABLE *B*

Comparative listings of the forest birds of Kuala Lompat and of lowland elevations on north-east Gunong Benom

i. Species found at Kuala Lompat, but not on Benom: *Pernis ptilorhynchus, Ixobrychus cinnamomeus, Ciconia stormi, Lophura erythrophthalma, Treron capellei, Treron olax, Ptilinopus jambu, Psittinus cyanurus, Cuculus vagans,* *Cacomantis variolosus, Chrysococcyx malayanus, Phoenicophaeus sumatranus, Centropus rectungis, Ninox scutulata, Eurostopodus temminckii, Hemiprocne longipennis, Harpactes kasumba, Harpactes orrhophaeus, Halcyon pileata, Anthracoceros malayanus, Anthracoceros coronatus, Micropternus brachyurus, Dinopium rafflesii, Muelleripicus pulverulentus, Dryocopus javensis, Corydon sumatrana, Pitta granatina, Pitta guajana, Coracina striata, Pericrocotus roseus, Pycnonotus eutilotus, Pycnonotus melanoleucos, Pycnonotus atriceps, Pycnonotus zeylanicus, Pycnonotus finlaysoni, Dicrurus aeneus, Platysmurus leucopterus, Trichastoma rostratum, Prinia rufescens, Orthotomus ruficeps, Orthotomus sutorius, Rhynomyias brunneata, Lanius tigrinus, Anthreptes malacensis, Nectarinia sperata, Gracula religiosa.*

ii. Species found at Kuala Lompat, not observed under 1000 ft on Benom but recorded there at higher elevations: *Rollulus rouloul, Nyctiornis amicta, Coracina fimbriata, Hypsipetes charlottae, Pomatorhinus montanus, Stachyris nigricollis, Orthotomus atrogularis, Muscicapa unicolor, Terpsiphone paradisii, Anthreptes singalensis, Arachnothera robusta.*

iii. Species found on Benom at 600–1000 ft, absent at Kuala Lompat (200–250 ft): *Ictinaetus malayensis, Microhierax fringillarius, Rhizothera longirostris, Macropygia ruficeps, Phaenicophaeus diardi, Rhyticeros undulatus, Meiglyptes tukki, Hemicercus concretus, Cymbirhynchus macrorhynchos, Pitta caerulea, Pitta sordida, Pericrocotus igneus, Aegithina lafresnayi, Chloropsis sonnerati, Pycnonotus squamatus, Pycnonotus cyaniventris, Pycnonotus erythophthalmos, Trichastoma sepiarium, Malacopteron affine, Stachyris nigriceps, Stachyris leucotis, Orthotomus sericeus, Enicurus ruficapillus, Rhipidura perlata, Aethopyga mystacalis, Dicaeum trigonostigma.*

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H. S. YONG

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YONG HOI SEN

School of Biological Sciences, University of Malaya, Kuala Lumpur

Pp. 155–163; 1 *Plate*

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By YONG HOI SEN

SYNOPSIS

Rattus rajah (Thomas) and *Rattus surifer* (Miller) are two medium sized spiny rats occurring in Malaysian forests which have proved difficult to distinguish by morphological characters, including external appearance and skeletal anatomy. Several authors have in fact combined them as a single polymorphic species.

Ecological data seem to indicate that these rats belong to separate species. Breeding and behaviour studies support this view. Karyotype and serological studies provide conclusive evidence for the distinctness of the two species.

THE names *Rattus rajah* (Thomas) and *Rattus surifer* (Miller) are applied to two medium-sized spiny rats occurring in Malaysian forests. The two taxa are phenetically rather alike and published opinions on their respective status differ. Bonhote (1903) regarded them as separate species belonging to the subgroup *rajah* of the *jerdoni* group. Chasen (1940) and Sody (1941), the principal revisers, retained both as full species. No firm opinion was offered by Tate (1936, 1947): "There appears to be a very strong resemblance between the many forms of the *rajah* group. One suspects that some will at length be shown as merely seasonal or age phases of single races". Ellerman (1949) attributed populations from Malaya to separate species under the names *R. rajah pellax* and *R. surifer surifer.* Ellerman and Morrison-Scott (1951), however, revised this opinion, and later (1955) suggested that *R. rajah* and *R. surifer* were probably conspecific. Harrison (1957, 1966) was inclined to take the same view: "This group is commonly divided into two forms, which may be called *R. rajah* and *R. surifer*, but there is some doubt about their being true distinct species. . . . Decision on the taxonomic question must be deferred until genetical and other studies are completed." Hill (1960), however, maintained that the two forms represented distinct species and clearly described the external features distinguishing them.

Although there is now no doubt that these rats can be readily distinguished by morphological characters (cf. Harrison, 1966), their systematic position, whether distinct species or a single polymorphic species, remains unsolved. It is the aim of this paper to provide an answer from various disciplines of comparative biological studies.

MATERIALS AND METHODS

All the rats used were trapped from the wild. Representatives of both were taken on Gunong Benom between 700–2500 ft, and additional specimens were collected at the following localities: Kampong Janda Baik, Bentong District, Pahang; 19th mile Genting Simpah and Bukit Lagong, Selangor; Maxwell's Hill, Taiping, Perak; Kaki Bukit, Perlis. Trapping was carried out in a variety of natural habitats and the field data recorded. Collectors's flesh (body) measurements and measurements of the cleaned skull of 21 *R. rajah* and 19 *R. surifer* were analysed statistically; differences between means were tested for significance by "Student's" *t*-test. This "classical" taxonomic approach was augmented by genetical studies including karyology and serology. Breeding experiments were also set up to test the crossability of these rats.

RESULTS

EXTERNAL MORPHOLOGY. Despite extensive overlap in all body dimensions (Table 1), the sample of *R. surifer surifer* shows a significantly greater mean head and body length ($0{\cdot}05 > P > 0{\cdot}02$), mean tail length ($0{\cdot}01 > P > 0{\cdot}001$), and mean hind foot length ($P < 0{\cdot}001$). The mean ear length, however, is not significantly different from that of *R. rajah pellax* ($0{\cdot}3 > P > 0{\cdot}2$).

TABLE 1

BODY DIMENSIONS OF *RATTUS RAJAH* AND *RATTUS SURIFER*

	Head & Body Length			Tail Length		
Species	Mean ± S.E. of Mean	C of V (%)	Obs. Range	Mean ± S.E. of Mean	C of V (%)	Obs. Range
R. rajah	174·29 ± 3·54	9·30	150–210	165·25 ± 3·88	10·51	132–200
R. surifer	187·32 ± 4·24	9·86	155–212	185·69 ± 4·33	9·32	157–215

	Hind Foot Length			Ear Length		
Species	Mean ± S.E. of Mean	C of V (%)	Obs. Range	Mean ± S.E. of Mean	C of V (%)	Obs. Range
R. rajah	37·86 ± 0·42	5·03	34–40	21·95 ± 0·71	4·66	20–23
R. surifer	42·21 ± 0·42	4·30	39–45	23·11 ± 0·68	4·05	22–25

	T : H & B (%)		
Species	Mean ± S.E. of Mean	C of V (%)	Obs. Range
R. rajah	94·91 ± 1·30	6·13	82·11–105·81
R. surifer	100·18 ± 1·57	6·26	91·51–112·12

S.E. = standard error
C of V = coefficient of variation
All measurements in millimetres

The pelage and tail colouration have been described in detail by Harrison (1957, 1966), Hill (1960) and Medway (1969). The two species are most readily distinguished by the presence in *R. surifer* of a sharp demarcating stripe on the flanks, formed by orange-tipped spines, and by the general body colouration.

SKULL ANATOMY. Various skull dimensions are given in Tables 2, 3 and 4. Of these only the mean length of anterior palatine foramina and the mean length of upper molar series between these rats differ significantly ($P < 0{\cdot}001$). There are

TABLE 2

SKULL DIMENSIONS OF *RATTUS RAJAH* AND *RATTUS SURIFER*

	Bulla Length			Palatal Length		
Species	Mean ± S.E. of Mean	C of V (%)	Observed Range	Mean ± S.E. of Mean	C of V (%)	Observed Range
R. rajah	4·76 ± 0·07	5·59	4·40–5·20	19·88 ± 0·41	7·94	17·80–23·45
R. surifer	4·79 ± 0·07	6·30	4·30–5·40	20·77 ± 0·27	5·40	17·35–22·60

	L. of Ant. Palatine Foramina		
	Mean ± S.E. of Mean	C of V (%)	Observed Range
R. rajah	5·94 ± 0·10	8·73	4·90–6·80
R. surifer	6·64 ± 0·09	8·07	5·35–7·70

All measurements in millimetres
C of V = Coefficient of Variation

TABLE 3

SKULL DIMENSIONS OF *RATTUS RAJAH* AND *RATTUS SURIFER*

	Occipitonasal Length			Length of Upper Molar Series		
Species	Mean ± S.E. of Mean	C of V (%)	Observed Range	Mean ± S.E. of Mean	C of V (%)	Observed Range
R. rajah	41·81 ± 0·81	7·22	37·70–48·20	6·82 ± 0·06	3·25	6·40–7·10
R. surifer	44·19 ± 0·57	5·45	37·40–48·20	6·47 ± 0·06	3·64	6·05–6·90

Species	Incisor-Molar L. / Palatal L.	Roots of Upper Molars
R. rajah	1	4,4,3;3,4,3;3,3,3
R. surifer	1	4,4,3;3,4,3;3,3,3

All measurements in millimetres
C of V = Coefficient of Variation

TABLE 4

DIMENSIONS OF SUBGENERIC CHARACTERS OF *RATTUS RAJAH* AND *RATTUS SURIFER*

		Bulla : Occ-nasal Length (%)		
Subgenus	Species	Mean ± S.E. of Mean	C of V (%)	Observed Range
Lenothrix	*R. rajah*	11·44 ± 0·14	4·90	10·42–12·27
	R. surifer	10·86 ± 0·16	6·26	10·05–12·83

		Palatal : Occ-nasal Length (%)		
Subgenus	Species	Mean ± S.E. of Mean	C of V (%)	Observed Range
Lenothrix	*R. rajah*	47·48 ± 0·32	2·65	44·65–49·48
	R. surifer	46·71 ± 0·91	1·63	45·02–48·34

		A.P.F. : Occ-nasal Length (%)		
Subgenus	Species	Mean ± S.E. of Mean	C of V (%)	Observed Range
Lenothrix	*R. rajah*	14·37 ± 0·18	6·87	12·76–16·14
	R. surifer	15·07 ± 0·15	5·83	13·20–16·72

Occ-nasal = Occipitonasal
A.P.F. = Anterior Palatine Foramina
C of V = Coefficient of Variation

no absolute differences between *rajah* and *surifer* in any of these characters. Other features of the skull such as general shape, shape of anterior palatine foramina, length of diastema, nasals, etc., also fail to demonstrate any morphological distinction.

HABITAT. *Rattus rajah* and *R. surifer* are found in the same general habitat, dipterocarp forests,* but are not normally present together (cf. Chasen, 1940). They occupy burrows in the ground, the entrances of which are loosely plugged with leaves. Trapping in Kampong Janda Baik, Genting Simpah, Maxwell's Hill, and Kaki Bukit produced only *R. surifer*, while trapping in Bukit Lagong and Gunong Benom yielded predominantly *R. rajah*. Only one *R. surifer* was trapped on Gunong Benom, where it was sympatric with *R. rajah* at an altitude of 2500 ft; 11 specimens of *rajah* were collected at this and lower altitudes.

BREEDING AND BEHAVIOUR. Both inter- and intra-specific crosses of *R. rajah* and *R. surifer* were unsuccessful under the prevalent animal-house conditions.

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*Characterized by the presence of trees belonging to the family Dipterocarpaceae; forest floor hard and carpeted with fallen leaves; base of trees without crevices; and typically with three-storied canopy.

In intra-specific pairs, the rats settled down with their mates immediately. By contrast, in interspecific pairs, when first brought together the rats either ignored their partner or reacted agonistically. No mating attempt was observed in either inter- or intra-specific pairs.

In interaction experiments, where at least two freshly-trapped members of the same species were introduced at the same time into the cage, individuals of the same species aggregated together, irrespective of sex. When new individuals were introduced after the original members had established themselves, these newly-introduced individuals sought out members of their own species and joined them in a common shelter. When the newly-introduced individuals belonged to an unrepresented species, they occupied fresh shelters and did not mix with the other species.

Although a surplus of jars serving as shelters (Figure 1) was provided, rats of the same species always aggregated together, leaving the other jars unoccupied. Even after being kept together for at least six months, the two species failed to mix (*cf.* Yong, 1970).

KARYOLOGY. The karyotypes of both *R. rajah* and *R. surifer* have been described (Yong, 1969). The chromosome number (2n) and the number of chromosome arms (N.F. or N.A.) are distinctly different. The sex chromosomes (both X and Y) in both, however, are of the same morphological type. The karyotypes of these rats are summarised in Table 5. The karyological differences cannot be explained in terms of polymorphism, and indicate that two disinct species are represented.

TABLE 5

KARYOTYPES OF *RATTUS RAJAH* AND *RATTUS SURIFER*

	Number of specimens examined		2n	Pairs of autosomes*			Allosomes		
Species	male	female		S	A	M	X	Y	FN**
Rattus rajah pellax	2	1	36	3	8	6	M	M	56
Rattus surifer surifer	2	2	52	2	19	4	M	M	66

*S = subterminal, A = acrocentric, M = metacentric
**FN = Fundamental Number (number of chromosome arms)

SEROLOGY. The one-dimensional starch-gel electropherograms for *rajah* and *surifer* sera and haemoglobins are shown in Figures 2 and 3. The albumin band of *R. rajah* moves at a slightly slower rate than that of *R. surifer* under the same experimental conditions (Figure 2), but is nevertheless species-specific. In addition, *R. rajah* possesses a pre-albumin band of constant mobility, which is absent in *R. surifer*. *R. rajah* also differs from *R. surifer* in the possession of an extremely slow-migrating band, just next to the point of application of serum sample.

R. rajah and *R. surifer* also differ in their haemoglobin electrophoretic patterns (Figure 3). *R. surifer* possesses two rather faint cathodal bands and one or two dark-staining anodal bands. *R. rajah*, on the other hand, possesses two well-defined anodal bands, and one or two rather faint cathodal bands. The cathodal bands in *rajah* seem to be polymorphic.

The faster haemoglobin band in *rajah* moves with a mobility slightly slower than its albumin band. The two anodal bands are species-characteristic, and are faster migrating than the anodal bands characteristic of *surifer*.

The species-specific albumin pattern of one dimension starch gel-electrophoresis is also borne out in agar-gel immunoelectrophoresis, employing anti-*sabanus* as well as anti-*muelleri* sera produced in rabbits. Species-characteristic reaction patterns are observed in *R. rajah* and *R. surifer* (Figure 4).

DISCUSSION

Although external morphological characters, such as those distinguishing *surifer* and *rajah*, are reliable for identification, they are not so useful in assessing relationship. "There are . . . a few kinds of characters, notably those of colour and colour pattern, that are almost always highly labile wherever encountered" (Simpson, 1961). However, the experimental evidence presented above shows that *R. rajah* and *R. surifer* exhibit species-characteristic behaviour. Members of *R. rajah* associated and did not mix with *R. surifer* under simulated natural conditions; and the same was true of *R. surifer*. In both cases, the rats consistently huddled together although excess shelters were available, and there was opportunity for them to separate into isolated individuals or pairs. No misassociation was observed. This behaviour under wild conditions would keep the rats distinct when present in the same locality. The failure to hybridize in the laboratory cannot be interpreted as strong support, since intra-specific pairings were equally unproductive.

Karyological and serological studies furnish further concrete evidence. The karyotypes and the serum-protein and haemoglobin electrophoretic patterns of *R. rajah* and *R. surifer* are species-specific. The marked karyotype differences between *R. rajah* and *R. surifer* would be effective in preventing hybridization. The multitude of proteins would ensure genetic incompatibility and hence effectively keep these rats distinct.

In sum, the evidences from external morphology, skull anatomy, ecology, breeding and behaviour studies, karyology, and serology verify the species status of *R. rajah* and *R. surifer*. These rats belong to distinct valid species and are not colour varieties of a single polymorphic species.

ACKNOWLEDGEMENTS

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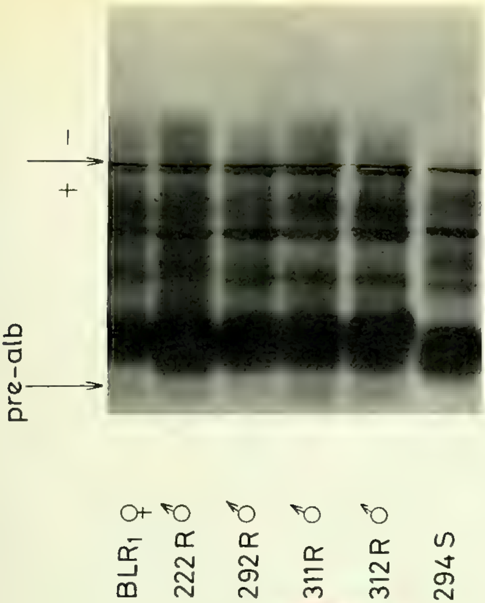
PLATE 1

FIG. 1. Glass jars provided as shelters (nesting site) for rat.

FIG. 2. One-dimension starch-gel serum electropherogram of *Rattus rajah* compared with *Rattus surifer* (294S). Borate buffers were used; gel buffer with pH 8·8 and bridge buffer with pH 8·3. Electrophoretic run : 18 hrs. at 100 volts. Stained with amido-black.

FIG. 3. One-dimension starch-gel haemoglobin electropherogram of *R. surifer* (GS1, 11·7S) and *R. rajah* (270R, BLR, 312), compared with *rajah* serum (222R). Electrophoretic run as in Fig. 2.

FIG. 4. Serum immunoelectropherogram of *R. rajah* and *R. surifer* against anti-*sabanus* serum.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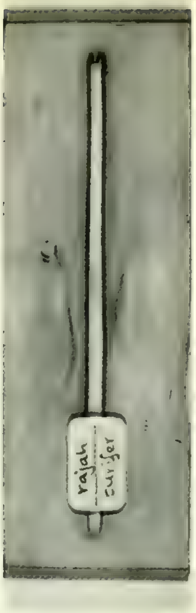
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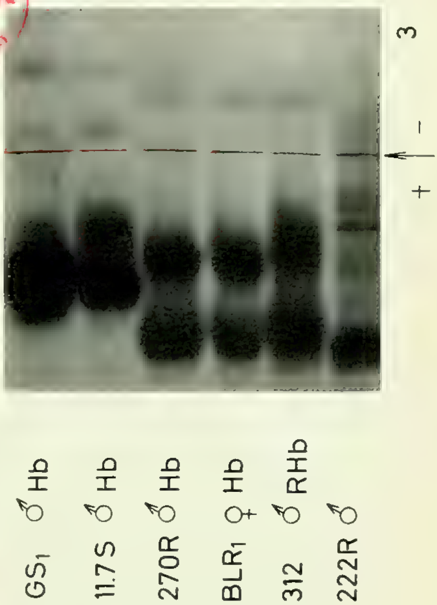
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11.7S ♂ Hb
270R ♂ Hb
BLR₁ ♀ Hb
312 ♂ RHb
222R ♂

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8. TICKS (IXODIDAE) OF GUNONG BENOM AND THEIR ALTITUDINAL DISTRIBUTION, HOSTS AND MEDICAL RELATIONSHIPS

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SYNOPSIS

Ticks collected on Gunong (Mt.) Benom, an undisturbed forest environment particularly favourable for studying altitudinal distribution (700 to 6916 ft) of tick species occurring in the Malay Peninsula, were *Ixodes granulatus*, *I. simplex*, *Haemaphysalis calvus*, *H. bispinosa*, *H. c. cornigera*, *H. hylobatis*, *H. nadchatrami*, *H. semermis*, *H. traguli*, *H. vidua*, *H. wellingtoni*, *H. asiatica*, *H. doenitzi*, *H. koningsbergeri*, *Dermacentor atrosignatus*, *D. compactus*, *Amblyomma testudinarium*, and *A. geomeydae*.

I. simplex and *H. calvus* were not previously recorded from the Malay Peninsula. *Haemaphysalis centropi* Kohls, 1949, is a synonym of the earlier described *H. doenitzi* Warburton and Nuttall, 1909. The species of *Dermacentor* in Malaya are reported for the first time.

No ticks were collected in mossy forests (5300–5500 ft). One found on a person at 6000 ft may have attached at a lower level. *Dermacentor atrosignatus* comprised 48% of the collections from vegetation between 500 and 2500 ft altitudes and 41% of those from 2600 to 5200 ft. *D. compactus* comprised 16% of collections from vegetation up to 2500 ft, but only 0·2% of those from higher altitudes. *H. nadchatrami* and *H. semermis* comprised 6 and 11%, respectively, of collections from vegetation between 500 and 2500 ft but 54% and 2% respectively, of those from 2600 to 5200 ft. Data are provided for tick parasitism of 28 mammal and bird species on Gunong Benom, for samples obtained by sweeping forest vegetation at different altitudes, and for vertebrates that were not tick-infested.

Species biting human beings were *H. nadchatrami*, *H. semermis*, *H. c. cornigera*, *Dermacentor atrosignatus*, and *A. testudinarium*. This mountain area is eminently suitable for investigating "primitive" cycles of tickborne viruses and rickettsiae in nature and many of the tick species listed are important candidates for epidemiological research. Elsewhere in Malaya, *I. granulatus* has been found to be infected by Langat and Lanjan viruses, *Dermacentor* sp. and *H. semermis* by Lanjan virus, and *H. nadchatrami* by Q fever (*Coxiella burneti*). Both haemaphysalid species, *Dermacentor* sp. and *I. granulatus* have been implicated in the natural cycle of tick typhus (*Rickettsia* sp.) in Malaya.

INTRODUCTION

MOUNT (Gunong) BENOM offers an exceptional opportunity for investigating the effects of altitude on ecological zonation in Malaya (Whitmore, 1972). The highest peak (6916 ft) in a compact montane formation, Gunong Benom is situated at approximately 4°N in the middle of Malaya between the Main and Eastern Ranges. Forest extending from 700 ft to the peak has been disturbed by logging operations only near the base and in scattered patches up to about 1700 ft. Ecologically, lowland forest merges with montane forest at 2500 ft and montane mossy forest begins at 5300 ft.

During the current Malayan Tick Survey[1], we have obtained considerable data concerning the distribution and host relationships of the ticks inhabitating lowlands and highlands of the Malay Peninsula. However, prior to the Gunong Benom Expedition (Medway, 1972), we had not had the opportunity to compare systematically the effects on tick distribution and incidence of altitudinal factors in a single unbroken, undisturbed Malayan transect such as this. Results from the Gunong

TABLE I

Ticks from vegetation on Gunong Benom, Pahang

Tick species	♂	♀	Nymph	Larva	Total	(%)
			Number			
500–2500 Feet altitude (Lowland forests)						
Dermacentor atrosignatus	103	158	0	0	261	(47·8)
Dermacentor compactus	40	46	0	0	86	(15·8)
Haemaphysalis nadchatrami	19	12	0	0	31	(5·7)
Haemaphysalis semermis	25	37	0	0	62	(11·3)
Haemaphysalis koningsbergeri	3	3	0	0	6	(1·1)
Haemaphysalis hylobatis	1	3	0	0	4	(0·7)
Haemaphysalis calvus	16	18	0	0	34	(6·2)
Haemaphysalis c. cornigera	18	21	3	0	42	(7·7)
Amblyomma testudinarium	7	5	2	0	14	(2·6)
Amblyomma geoemydae	0	0	6	0	6	(1·1)
Total	232	303	11	0	546	
2600–5200 Feet altitude (mountain forests)						
Dermacentor atrosignatus	63	109	0	0	172	(41·4)
*Dermacentor compactus**	0	1	0	0	1	(0·2)
Haemaphysalis nadchatrami	110	113	0	0	223	(53·6)
Haemaphysalis semermis	3	7	0	0	10	(2·4)
Haemaphysalis hylobatis	0	1	0	0	1	(0·2)
Amblyomma testudinarium	5	4	1	0	9	(2·2)
Total	181	234	1	0	416	
5300—5500 Feet altitude (Mountain mossy forests)						
(No ticks)**	0	0	0	0	0	(0·00)

*Collected at 2700 ft.

**5 persons sweeping 24 March (1500–1800 hrs), 25 March (1000–1500 hrs), 26 March (1100–1400 hrs), 14 January (1400–1800 hrs), 15 January (0900–1300 hrs).

---

[1] The Malayan Tick Survey, which has been in operation since mid-1966, is a collaborative study between the Institute for Medical Research, Kuala Lumpur, the Zoology Department, University of Maryland, and NAMRU-3, Cairo, supported in part by U.S. Army Research and Development Command grant number DADA-17-67-C-7003.

Benom study have been particularly useful in providing material and data for the first author's revisional study of the *Dermacentor* ticks of Southeast Asia and of the biology and distribution of *Haemaphysalis* ticks of the world.[2]

The University of Malaya – British Museum (Natural History) – sponsored Gunong Benom Expedition, headed by Lord Medway, who has described (1972) previous exploration of the area, expedition aims and operations, and participating organizations and personnel, was in the field from 1 February to 15 April 1967. Members of the George W. Hooper Foundation of the University of California Medical Center, San Francisco, then attached to the Faculty of Medicine, University of Malaya, participated in the expedition and later revisited the mountain for additional collecting (Marchette, 1967; Dr. Richard Garcia, personal communication). Certain members of the Malayan Tick Survey also collaborated with the expedition and worked in the area prior to and following the period the expedition was on Gunong Benom. The names of persons responsible for the excellent tick collections and data reported here are listed at the end of this paper. The outline description of forest zones on northeast Gunong Benom by Whitmore (1972) should be consulted by readers who are particularly concerned with the ecological aspects of this study.

The term Malaya, as used in this paper, refers only to the Malay Peninsula from the Southern border of Thailand to Singapore. In discussions of Borneo, political divisions are not mentioned.

MATERIALS AND METHODS

Vertebrate animals collected by members of the Gunong Benom expedition or the Malayan Tick Survey were routinely inspected for ectoparasites. For ticks, bath towels attached to a stick were also used to flag vegetation at intervals from 700 to 5500 ft. Owing to the absence of ticks between 5300 and 5500 ft, and the cold, wet weather above this altitude, no effort was made to collect material between 5500 ft and the peak at 6916 ft. Actual dates of collection of each specimen are available and will be furnished on request.

RESULTS

The ticks of Malaya have been reviewed by Kohls (1957) and by Audy et al. (1960). Subsequent changes in the taxonomic status of certain *Haemaphysalis* species are mentioned below. The reader is referred to these papers for taxonomic details, which are omitted in this report. Results are presented in tabular form for ticks taken by flagging vegetation at various altitudes (Table 1) and for those from hosts (Table 2), together with a list of vertebrate species that were apparently not tick-infested.

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[2] The *Dermacentor* and *Haemaphysalis* studies are supported in part by contract number 03-005-01 between the U.S. Public Health Service National Institute of Allergy and Infectious Diseases, Bethesda, Maryland, and NAMRU-3, Cairo.

TABLE 2

Ticks from vertebrates on Gunong Benom, Pahang*

500–2500 Feet altitude (Lowland forests)

Vertebrate species	Number examined	Number infested	Tick species (sex/stage)
INSECTIVORA			
Echinosorex gymnurus	1	1	*Ixodes granulatus* (4♀, 3N, 4L) *Amblyomma* sp. (1L)
CHIROPTERA			
Penthetor lucasi	1	1	*Ixodes simplex* (1L)
Rhinolophus stheno	24	11	*Ixodes simplex* (6♀, 2N, 5L)
Rhinolophus affinis	6	6	*Ixodes simplex* (3♀, 2N, 4L)
RODENTIA			
Ratufa affinis	7	1	*Dermacentor* sp. (1N)
Callosciurus caniceps	3	1	*Dermacentor atrosignatus* (2N)
Sundasciurus tenuis	9	1	*Haemaphysalis nadchatrami* (2N)
Rhinosciurus laticaudatus	3	1	*Haemaphysalis nadchatrami* (11N)
Lariscus insignis	3	2	*Haemaphysalis ?koningsbergeri* (2N)
Rattus sabanus	40	17	*Ixodes granulatus* (1♀) *Haemaphysalis nadchatrami* (3N, 25L) *Dermacentor atrosignatus* (4N) *Dermacentor* sp. (2N, 29L)
Rattus muelleri	5	1	*Ixodes granulatus* (1♂, 1♀)
Rattus bowersii	2	2	*Amblyomma* sp. (1L) *Dermacentor atrosignatus* (1N) *Dermacentor* sp. (16L) *Haemaphysalis nadchatrami* (1N) *Haemaphysalis semermis* (3N, 1L)
Rattus rajah	7	1	*Dermacentor* sp. (1L) *Haemaphysalis nadchatrami* (1N)
Rodent burrow	40	1	*Ixodes granulatus* (12L)
CARNIVORA			
Felis bengalensis	1	1	*Haemaphysalis asiatica* (1♂) *Haemaphysalis koningsbergeri* (14♂) *Haemaphysalis semermis* (1♂)
Arctiogalidia trivirgata	1	1	*Haemaphysalis koningsbergeri* (2♂)
Arctictis binturong	1	1	*Haemaphysalis koningsbergeri* (26♂, 2♀) *Haemaphysalis semermis* (1♂) *Haemaphysalis hylobatis* (2♂)
Hemigalus derbyanus	1	1	*Haemaphysalis koningsbergeri* (1♂) *Haemaophysalis vidua* (3N, 26L)
Paradoxurus hermaphroditus	1	1	*Haemaphysalis koningsbergeri* (1♀)
Domestic dog (Lord Medway)	–	–	*Dermacentor* sp. (4L) *Haemaphysalis koninigsbergeri* (7♂, 8♀) *Haemaphysalis semermis* (3♂)
Domestic dogs (aborigine village)	15	6	*Haemaphysalis bispinosa* (8♂, 5♀, 4N) *Haemaphysalis koningsbergeri* (3♂, 9♀)

Vertebrate species	Number examined	Number infested	Tick species (sex/stage)
Artiodactyla			
Tragulus javanicus	4	4	*Dermacentor* sp. (1N)
			Haemaphysalis nadchatrami (4N)
			Haemaphysalis semermis (1♂, 2N, 1L)
			Haemaphysalis traguli (1♂, 2♀, 5N, 5L)
Tragulus napu	1	1	*Haemaphysalis ?nadchatrami* (1L)
Sus scrofa	2	2	*Amblyomma testudinarium* (1N)
			Dermacentor atrosignatus (27♂, 9♀)
			Dermacentor compactus (11♂, 5♀)
			Haemaphysalis nadchatrami (18♂, 5♀)
			Haemaphysalis semermis (2♂, 1♀)
Aves			
Centropus sinensis eurycercus	2	2	*Amblyomma* sp. (1N)
			Amblyomma geomeydae (1N)
			Haemaphysalis doenitzi (1♂)
Dendrocopos m. moluccensis	1	1	*Haemaphysalis doenitzi* (2L)
Argusianus argus	1	1	*Haemaphysalis wellingtoni* (2N, 1L)
Lophura erythrophthalma	1	1	*Haemaphysalis wellingtoni* (2♂, 10L)
Anthracoceros malayanus	1	1	*Amblyomma* sp. (1N)
Human beings (biting)**			*Amblyomma testudinarium* (1N)
			Dermacentor atrosignatus (1N)
			Haemaphysalis c. cornigera (1♀)
			Haemaphysalis nadchatrami (2♀)
			Haemaphysalis semermis (1♂, 2N)
Human beings (crawling on)			*Amblyomma testudinarium* (1♂, 2♀)
			Dermacentor atrosignatus (1♂, 1N)
			Haemaphysalis nadchatrami (2♀)
			Haemaphysalis semermis (2♀)
2600–6000 Feet altitude (Mountain forests)			
Rodentia			
Rattus inas (3600 ft)	4	1	*Haemaphysalis nadchatrami* (1N)
Human being (biting, 6000 ft)**			*Haemaphysalis nadchatrami* (1♀)
Human being (crawling on, 3000 ft)			*Haemaphysalis hylobatis* (1♀)

*The 243 vertebrates (representing 53 forms) inspected and not found to be tick infested, and their numbers (in parentheses), were:

500–2500 Feet altitude (Lowland forests)

Primates. *Tupaia minor* (1), *T. glis* (2), *Ptilocercus lowii* (2), *Nycticebus coucang* (1), *Macaca fascincularis* (1), *Presbytis obscurus* (5).

Chiroptera. *Cynopterus brachyotis* (11), *C. horsfieldi* (22), *Eonycteris spelaea* (18), *Chironax melanocephalus* (1), *Macroglossus lagochilus* (6), *Balionycteris maculata* (3), *Rhinolophus macrotus* (2), *R. refulgens* (12), *Emballonura monticola* (12), *Hipposideros diadema* (2), *H. galeritus* (2).

Rodentia. *Hylopetes spadiceus* (4), *Pteromyscus pulverulentus* (1), *Petaurista petaurista* (11), *P. elegans* (4), *Aeromys tephromelas* (4), *Iomys horsfieldi* (5), *Sundasciurus lowi* (4), *S. tenuis* (8), *S. hippurus* (2), *Callosciurus notatus* (14), *C. nigrovittatus* (4), *C. caniceps* (1), *C. prevosti* (1), *Rhinosciurus laticaudatus* (2), *Lariscus insignis* (1), *Ratufa bicolor* (6), *R. affinis* (6), *Rattus cremoriventer* (7), *R. sabanus* (15), *R. bowersii* (1), *R. rajah* (6), *R. inas* (3), *R. canus* (2), *R. whiteheadi* (6), *Chiropodomys gliroides* (1).

Reptilia. *Varanus salvator* (1), *V. rudicollis* (1), *Gonocephalus boreensis* (1).

Aves. *Otus rufescens* (1), *Chrysocolaptes validus* (1), *Arachnothera longirostra* (1), *Anorrhinus galeritus carinatus* (1).

2600–5300 Feet altitude (Mountain forests)

Rodentia. *Sundasciurus tenuis tahan* (3), *Callosciurus flavimanus* (1), *Rattus edwardsi* (7), *R. tiomanicus jalorensis* (3).

**Also see remarks in text on larvae (presumably *A. testudinarium*), infesting persons at 3000 to 4000 foot altitudes during the wet season but not during the dry month of February.

Ixodes granulatus Supino

I. granulatus was collected at 700 and 800 ft from the single moonrat (Insectivora, Erinaceidae, *Echinosorex gymnurus*) and from 2 rodents, *Rattus sabanus* and *R. muelleri*. The moonrat, trapped on 28 February beside a stream, was parasitized by 4 female *I. granulatus* on the dorsum and 3 nymphs and 4 larvae on the thighs and belly. One male and 1 female infested 1 of 5 *R. muelleri* (3 March) and 1 female infested 1 of 25 *R. sabanus* (12 January). Twelve larvae resting on the roof of a rodent burrow dropped to a black plate (used for collecting chiggers) a few moments after the plate was inserted by Nadchatram into 1 of 40 burrows on Gunong Benom. Notably, the infestation rate of this tick species on the mountain at the times of collection was low; squirrels and several other rodents were not infested.

I. granulatus commonly parasitizes small mammals, and sometimes birds, living on the ground or in trees in forests from Southeast Asia (southern China, Vietnam, Okinawa, Borneo, Indonesia) to eastern India (Assam). The life cycle of this 3-host tick under laboratory conditions was described by Nadchatram (1960). This is the only Malayan tick species in which each developmental stage parasitizes rodents. The nidicolous behaviour of *I. granulatus* has been confirmed by Nadchatram in several areas of Malaya (unpublished data.)

I. granulatus from *Rattus muelleri* and *R. sabanus* in the Ulu Langat Forest Reserve, Selangor, was the original source of the virus causing Langat encephalitis of humans (Smith, 1956; Hoogstraal, 1966). The natural history of Langat virus remains to be studied. *I. granulatus* is also involved in the cycles of tick typhus (*Rickettsia* sp.) and Q fever (*Coxiella burneti*) in climax forests of Malaya (Marchette, 1966). Specimens from Trengganu have yielded Lanjan virus (N. J. Marchette, personal communication). Only a single specimen of *I. granulatus* has been recorded biting man in Malaya. Thus, this species plays no important direct role in the epidemiology of human disease. However, many other ticks, among them species that more or less frequently infest human beings, feed on the same hosts and may acquire pathogens circulated in a *granulatus* – rodent – *granulatus* cycle and transmit these disease agents to other hosts during feeding in subsequent developmental stages. The potential indirect epidemiological role of *I. granulatus* should be especially interesting to investigate.

Ixodes simplex Neumann

Bats parasitized by *I. simplex* were *Penthetor lucasi* (1 larva from 1 examined, 3600 ft), *Rhinolophus stheno* (6 females, 2 nymphs, 5 larvae, from 11 of 24 examined between 700 and 900 ft), and *R. affinis* (3 females, 2 nymphs, 4 larvae, from 6 of 6 examined at 1500 ft). Eleven other bat species (91 specimens) between 500 and 2500 ft were free of ticks. These are the first published records of *I. simplex* from Malaya and from the genus *Penthetor*.

I. simplex infests many microchiropteran bats, chiefly in the genera *Rhinolophus*, *Myotis*, and *Miniopterus*, in Africa, Europe, Asia and Australia. Other (unpublished)

Malayan records are from *R. stheno* and *Miniopterus medius* at Karak and Fraser's Hill, Pahang. The disease relationships of *I. simplex* have not been investigated.

Haemaphysalis calvus Nuttall and Warburton

Sixteen male and 18 female *H. calvus* were found on lowland forest vegetation in Kuala Kerau and Kuala Lompat Forest Reserves. This species is known only from the original collection from a buffalo in northern Borneo, and from our collections (unpublished) from forest vegetation in Kedah, Pahang, and Selangor, from a tame sambar deer (*Cervus unicolor*) and a tiger [British Museum (Natural History)] in Pahang, and from a bear near Bangkok, Thailand. Disease relationships have not been studied.

Haemaphysalis bispinosa Neumann

Eight males, 5 females, and 4 nymphs were taken from 6 of 15 domestic dogs examined in Kuala Kerau Forest Reserve in September 1966. These dogs belonged to aborigine villagers and should be recognized as a source distinct from Lord Medway's pet dog, which accompanied Gunong Benom Expedition members and yielded ticks characteristic of wild forest-dwelling carnivores.

In Malaya, *H. bispinosa* shows all the biological features of an introduced parasite, being associated entirely with domestic animals (Hoogstraal et al., 1969). In its homeland, Ceylon, India, southern Nepal, and western Burma, *H. bispinosa* commonly parasitizes wild and domestic birds and mammals. The long list of disease relationships attributed to this species in much literature from Asia, Australia, New Zealand, Japan, and Pacific islands is completely erroneous, having been assembled from studies of misidentified ticks (Hoogstraal et al., 1968). The true disease relationships of *H. bispinosa* remain to be determined.

Haemaphysalis cornigera cornigera Neumann

Specimens collected in Kuala Kerau and Kuala Lompat Forest Reserves at the southeast base of Gunong Benom by the Malayan Tick Survey were: (September 1966) 16 males, 13 females, 3 nymphs from forest vegetation, 1 female, biting person; (April 1968); 2 males, 8 females from forest vegetation.

H. c. cornigera is widely but apparently erratically distributed in Malayan forests, where adults parasitize various kinds of deer, and wild pigs and carnivores. Nymphs and larvae feed on forest rodents. This parasite is common in Borneo and Indonesian islands. Its northern distributional limits and disease relationships remain to be investigated.

Haemaphysalis hylobatis Schulze

Eight specimens were taken, 2 males from the bear cat, *Arctictis binturong*, at 700 ft, 1 female crawling on a man at 3000 ft, 1 male and 3 females from lowland forest vegetation, and 1 female from mountain forest vegetation (2700 ft).

H. hylobatis is an infrequently encountered tick of Malaya and Sumatra, and the 8 from Gunong Benom comprise the largest known number from any single locality. This deep-forest parasite, infests monkeys, man, and carnivores, including domestic dogs, in Pahang, Selangor, and Kedah, Malaya, and in Sumatra, Indonesia. A female reared from a nymph infesting *Rattus surifer* in Selangor (Audy et al., 1960) is the only previously published record of this species in Malaya, and the only available data for immature stage hosts. The disease relationships of *H. hylobatis* have not been studied.

Haemaphysalis nadchatrami Hoogstraal, Trapido and Kohls

Collections from sweeping forest vegetation and from hosts (examined/infested) at various altitudes are as follows:

Rattus sabanus (40/5), 700 to 950 ft, 3 nymphs, 25 larvae
Rattus bowersii (2/1), 800 ft, 1 nymph
Rattus rajah (7/1), 1700 ft, 1 nymph
Rattus inas (4/1), 3600 ft, 1 nymph
Sundasciurus tenuis (9/1)., lowlands, 2 nymphs
Rhinosciurus laticaudatus (3/1), 800 ft, 11 nymphs
Sus scrofa, (2/2) 800 and 1400 ft, 18♂, 5♀
Tragulus napu (1/1), lowlands, 1 larva (tentative identification)
Tragulus javanicus (4/2), lowlands, 4 nymphs
Domestic dogs (aborigine village) (15/2), lowlands, 1♂, 1♀
Man (biting), 750 and 6000 ft, 2♀
Man (crawling on), 750 ft, 1♀
Vegetation, 500 to 2500 ft, 23♂, 22♀
Vegetation, 2600 to 5200 ft, 110♂, 113♀

H. nadchatrami larvae and nymphs feed on forest rodents and other small mammals Usually rather few are collected from hosts, presumably owing to especially short periods of parasitism. Adults feed on wild pigs, deer, carnivores, and man. As usual, the 2 wild pigs (*Sus scrofa*) examined were infested by a number of *H. nadchatrami* adults. Sweeping forest vegetation in all parts of Malaya almost always yields questing adults of this species. Notably, adults were much more numerous on vegetation on Gunong Benom at 2600 ft and above than below this elevation (Table 1). All samples, particularly those from higher elevations, were at the upper range of robustness for this species. The Gunong Benom forest environment is obviously ideal for *H. nadchatrami*. The comparative incidence in Malaya of this species and of *H. semermis* is discussed in the section on the latter species.

One of the 2 females biting humans was attached to the ankle, under the sock; a large patch of host skin remains surrounding the hypostome. The second discovered on a person near camp 5 at 6000 ft, may have attached at a lower altitude.

H. nadchatrami, a common forest dweller from central Thailand through the Malay Peninsula to Borneo, Java, Sumatra, and adjacent islands of Indonesia (Hoogstraal, Trapido, and Kohls, 1965), also occurs in the Phillipines on Palawan Island near Borneo (Hoogstraal, Kohls, and Parrish, 1968). In Malaya, adults have been found the year around. While there is probably a seasonal peak in population numbers, this has not yet been demonstrated.

Owing to its ubiquity, wide range of immature and adult stage hosts including man, and year-round feeding activity, *H. nadchatrami* is highly suspect as a reservoir and vector of viruses and rickettsiae. The "*Haemaphysalis* spp." in Marchette's (1966) study of Malayan tick typhus obviously consisted of many *H. nadchatrami* (Hoogstraal, 1967). Specimens of this species from Trengganu have yielded *Coxiella burneti*, the agent of Q fever (N. J. Marchette, personal communication). During the Malayan Tick Survey, 7 males and 4 females, in addition to those listed here, were collected while biting man.

Haemaphysalis semermis Neumann

Collections from sweeping forest vegetation and from hosts (examined/infested) at various altitudes are as follows:

Rattus bowersii (2/2), 800 ft, 3 nymphs, 1 larva
Felis bengalensis (1/1), 800 ft, 1♀
Arctictis binturong (1/1), 700 ft, 1♂
Domestic dog (Lord Medway's), 700 ft, 3♂
Domestic dogs (aborigine village) (15/6), lowlands, 8♂, 11♀, 5 nymphs
Sus scrofa (2/2), 800 and 1400 ft, 2♂, 1♀
Tragulus javanicus (4/1), lowlands, 1♂, 2 nymphs, 1 larva
Man (biting), 800 ft, 1♂, 2 nymphs
Man (crawling on), 700 and 1000 ft, 3♀
Vegetation, 500 to 2500 ft, 47♂, 53♀
Vegetation, 2600 to 5200 ft, 3♂, 7♀

The host range of *H. semermis* and *H. nadchatrami* is the same, though preferred hosts appear to be carnivores for *semermis* and wild pigs for *nadchatrami*. The 2 species are practically always sympatric in Malaya, and often on the same hosts. Of the 2259 adults of these 2 species in our Malayan collections, 1589 (70%) are *nadchatrami* and 670 (30%) are *semermis*. Of the 427 adults of these 2 species from Gunong Benom, 286 (67%) are *nadchatrami* and 141 (33%) are *semermis*.

The distribution of *H. semermis*, from southern Thailand through the Malay Peninsula and adjacent islands to Borneo and Sumatra, is almost the same as that of *H. nadchatrami* (Hoogstraal, Trapido, and Kohls, 1965).

The remarks on potential medical relationships of *H. nadchatrami* apply equally to *H. semermis*. Specimens of *H. semermis* from Trengganu have yielded Lanjan virus (N. J. Marchette, personal communication).

Haemaphysalis traguli Oudemans

The 4 larger mouse-deer, *Tragulus javanicus*, examined in the lowland forests of Gunong Benom were infested by 1 male, 2 females, 5 nymphs, and 5 larvae of *H. traguli*. (The single smaller mouse-deer, *T. napu*, was parasitized by only a larva of *H. ?nadchatrami*.)

Adults and immature stages of *H. traguli* commonly feed on *Tragulus javanicus* and *T. napu* in forests of Malaya, and also in Indonesia, Borneo, Thailand, and Burma (Hoogstraal, 1966). The subgeneric position of this and the related *H. vidua* is uncertain. The disease relationships of *H. traguli* have not been investigated.

Haemaphysalis vidua Warburton and Nuttall

Three nymphs and 26 larvae of *H. vidua* were taken on a banded palm civet, *Hemigalus derbyanus*, at 900 ft.

This rare tick is known only from various species of civets (Viverridae) in Pahang, Malaya, and near Kalabakan, Borneo (Hoogstraal, 1962, 1964). Disease relationships have not been studied.

Haemaphysalis wellingtoni Nuttall and Warburton

Two nymphs and 1 larva were taken from an argus pheasant, *Argusianus argus*, in lowland Kuala Lompat Forest Reserve on 12 March 1966. Two males and 10 larvae were found among the ear coverts of a crestless fire-back pheasant, *Lophura erythropthhalma*, in the same locality the same week.

H. wellingtoni ranges from Ceylon, Andaman Islands, and India through southern Nepal, Burma, Thailand, Vietnam, and Malaya, to Borneo and Indonesia (reports from New Guinea are incorrect). All stages typically parasitize wild and domestic gallinaceous birds. Other ground-feeding birds, and sometimes small mammals, are less frequently infested. The migratory habits of some hosts undoubtedly account for the extraordinarily wide distribution of *H. wellingtoni* and specimens have been found in Japan on a migrant gray thrush, *Turdus c. cardis*.

The disease relationships of *H. wellingtoni* unfortunately have not been studied This species is an especially interesting candidate for arbovirus investigation.

Haemaphysalis asiatica (Supino)

A single male of this uncommon species was taken on a leopard cat, *Felis bengalensis*, at 750 ft.

H. asiatica [= *H. dentipalpis* Warburton and Nuttall] occurs in forests of Burma, southern China, Vietnam, Thailand, peninsular Malaya, and Borneo, where its chief hosts are civets (Viverridae) and, less often, other carnivores (Hoogstraal and Trapido, 1966). The disease relationships of this species have not been studied.

Haemaphysalis doenitzi Warburton and Nuttall

Two of the 9 birds examined on Gunong Benom were infested by *H. doenitzi*. These were a coucal, *Centropus sinesis*, by a male (700 ft), and a short-tailed babbler, *Trichastoma malaccense*, by 2 larvae (1500 ft).

H. doenitzi adults and immature stages infest birds in forests from Ceylon and southern India to Borneo, Indonesia, New Guinea, southern China, Laos, Vietman, Taiwan, and southern Japan (Hoogstraal, unpublished data). Coucals, gallinaceous birds, and other birds that feed on or close to the ground are frequent hosts. Some records from Thailand and Laos are from mammals (leporids and domestic dogs.) *H. centropi* Kohls (1949) is a synonym of *H. doenitzi* Warburton and Nuttall (1909) (Hoogstraal, unpublished). The disease relationships of this widely-ranging species unfortunately have not been investigated.

Haemaphysalis koningsbergeri Warburton and Nuttall

Collections from sweeping forest vegetation and from hosts (examined/infested) are as follows:

Lariscus insignis (3/2), 700 and 800 ft, 2 nymphs (tentative identification)
Felis bengalensis (1/1), 800 ft, 14♂
Arctiogalidia trivirgata (1/1), 750 ft, 2♂
Arctictis binturong (1/1), 700 ft, 26♂, 2♀
Hemigalus derbyanus (1/1), 900 ft, 1♂
Paradoxurus hermaphroditus (1/1), lowlands, 1♀
Domestic dog (Lord Medway's), 750 and 800 ft, 7♂, 8♀
Domestic dogs (aborigine village) (15/6), lowlands, 3♂, 9♀
Vegetation, 500 to 2500 ft, 3♂, 3♀

Adults of *H. koningsbergeri* are common parasites of all wild carnivores and of domestic dogs in Malayan forests. Exceptional hosts (unpublished) are the mousedeer (*Tragulus javanicus* and *T. napu*), wild pig (*Sus scrofa*), pangolin (*Manis javanica*), and domestic goat. A single record, possibly erroneous, is from domestic fowl. Among our numerous records of this species, none is from man. The immature stages have not been reared in the laboratory and identification of nymphs and larvae, from squirrels and *Rattus*, is tentative.

Adults are frequently obtained by sweeping forest vegetation, but in comparatively small numbers that appear not to indicate the true incidence of *H. koningsbergeri* in Malayan forests. The questing position and location of adults on vegetation, possibly closer to the ground than usually reached in sweeping, should be investigated.

The range of this species includes Borneo, Java, Sumatra, and nearby islands. It would be interesting to know the capacity of *H. koningsbergeri* to transmit *Babesia* spp. among carnivores and to serve as a vector of viruses and rickettsiae.

"***Dermacentor auratus*** group"

The true *D. auratus* Supino is rare in Malaya. We have records of *D. auratus* only from Johore (Bekok Forest Reserve, Gunong Sumalayang, and Gunong Berembang), Trengganu (Bukit Kedap Forest Reserve and Bukit Bintang Besut), Perak (Sungei Klah Forest Reserve), and Pahang (Petoh Forest Reserve). The "*D. auratus*" or "*D. auratus* group" ticks earlier reported in literature on tickborne pathogens in Malaya refer in fact to *D. astrosignatus* or *D. compactus*, or to both, but not to *D. auratus* (*sensu strictu*). *Dermacentor* ticks are involved in the cycles of tick typhus (*Rickettsia* sp.) and of Q fever (*Coxiella burneti*) in Malayan climax forests (Marchette, 1966). Immature *Dermacentor* from rodents from Bukit Lanjan, 7 miles from Kuala Lumpur, provided the first isolation of Lanjan virus (Smith *et al.*, 1967).

The following specimens from Gunong Benom cannot be identified to species and are considered as "*Dermacentor* sp."

Ratufa affinis (7/1), 1200 ft, 1 nymph
Rattus sabanus (40/11), 700 to 2200 ft, 2 nymphs, 29 larvae
Rattus rajah (7/1), 1700 ft, 1 larva
Rattus bowersii (2/1), 800 ft, 16 larvae
Tragulus javanicus (4/1), lowlands, 1 nymph
Domestic dog (Lord Medway's), 700 ft, 4 larvae

Dermacentor atrosignatus Neumann

Collections from sweeping forest vegetation and from hosts (examined/infested) are as follows:

Callosciurus caniceps (3/1), 700 ft, 2 nymphs
Rattus sabanus (40/11), 700 to 2200 ft, 4 nymphs
Rattus bowersii (2/1), 800 ft, 1 nymph

Sus scrofa (2/2), 800 and 1400 ft, 27♂, 9♀
Man (biting), 1700 ft, 1 nymph
Man (crawling on), 750 and 2500 ft, 1♂, 1 nymph
Vegetation, 500 to 2500 ft, 161♂, 243♀
Vegetation, 2600 to 5200 ft, 63♂, 109♀

These 613 adult specimens comprise 84% of the 731 adult *Dermacentor* ticks taken on Gunong Benom (see also Tables 1–3).

The wild pig, *Sus scrofa*, appears to be the chief host of all adult *Dermacentor* in Malaya, and probably of most if not all *Dermacentor* species of tropical Asia. *Sus scrofa* is the most common and generally distributed large mammal in Malayan forests. In the absence of wild pigs, *Dermacentor* ticks would probably be rare in this environment. The 2 wild pigs examined on Gunong Benom yielded 52 adult *Dermacentor*, of which 36 (69%) were *D. atrosignatus* and 16 (31%) *D. compactus*. The 530 wild pigs examined throughout Malaya (Table 3) yielded 8294 adult *Dermacentor*, of which 5498 (66%) were *D. astrosignatus* and 2796 (34%) *D. compactus*. More males (61%) than females (39%) were found on wild pigs owing to the male's longer attachment period and the female's shorter feeding period. In collections of questing adults from Malayan forest vegetation, females (58%) outnumbered males (42%) (Table 3), as they did on Gunong Benom.

TABLE 3

Adult *Dermacentor atrosignatus* and *D. compactus* specimens from all Malayan sources (Hoogstraal collection, 20 April 1969)

Source	*D. atrosignatus*		*D. compactus*		Total ♂ & ♀		Total adults
	♂	♀	♂	♀	♂	♀	
Vegetation	3,725	4,756	1,631	2,650	5,356	7,406	12,762
Sus scrofa (530)	3,365	2,133	1,700	1,096	5,065	3,229	8,294
Other hosts (27)	22	43	7	14	29	57	86
Human beings (8)							
crawling on	3	2	0	1	3	3	6
biting	0	1	1	0	1	1	2
Total	7,115	6,935	3,339	3,761	10,454	10,696	21,150
% adults	66		34				

Immature-stage hosts of *Dermacentor* ticks in Malaya are various small size mammals such as insectivores, squirrels and other rodents, carnivores, muntjac, mouse-deer, domestic goats and dogs, and man. Our data for about 800 Malayan nymphs and larvae are not sufficiently extensive or representative to permit discussion of comparative importance of different mammal species as immature-stage hosts. Human beings are seldom recorded as hosts in Malaya in our data and by

Audy *et al.* (1960). This is in marked contrast to the incidence of human infestation by the true *D. auratus* (Supino) in India and the terai (lowlands) of Nepal (Hoogstraal, 1970).

Most *Dermacentor* specimens in our Malayan tick collections are from altitudes below 2500 ft. On Gunong Benom, the 2500 ft altitudinal level appears to be the upper limit of distribution of *D. compactus*, except for an occasional straggler to 2700 ft. On this mountain, tick collections from vegetation up to 2500 ft consisted of 261 (75%) *D. atrosignatus* and 86 (25%) *D. compactus* (Table 1). Above this level, however, these percentages were 41 and 0·24, respectively. The only *D. compactus* specimen taken in the montane forest range was a female at 2700 ft.

Different altitudinal distribution results for *Dermacentor* ticks were obtained on Mt. Ophir, (= Gunong Ledang), Johore, about 125 miles south of Gunong Benom (Malayan Tick Survey data, September 1968). On Mt. Ophir, *D. compactus* appears to be more numerous in relation to *D. atrosignatus* than in any other Malayan locality known to us. Of 1253 ticks of both species taken from Mt. Ophir forest vegetation, 698 (56%) were *D. atrosignatus* and 555 (44%) were *D. compactus*. The altitudinal distribution of these samples was as follows.

altitude (ft)	number collections	number *D. atrosignatus*	(%)	number *D. compactus*	(%)	total
1000	3	98	(50%)	97	(50%)	195
1500	4	155	(64%)	86	(36%)	241
2000	5	217	(68%)	103	(32%)	320
2500	3	73	(38%)	119	(62%)	192
3000	1	8	(42%)	11	(58%)	19
3500	4	114	(54%)	99	(46%)	213
4000	2	33	(45%)	40	(55%)	73
total	22	698	(56%)	555	(44%)	1253

The 46 to 58 percentages recorded for *D. compactus* in relation to *D. atrosignatus* at altitudes above 2500 ft on Mt. Ophir are in sharp contrast to the data from Gunong Benom. A comparative environmental study of altitudinal forest zones on Gunong Benom and Mt. Ophir might yield data showing the basic ecological requirements of each species and reasons for the disproportionate numbers of *D. compactus* at all levels and especially at upper elevations of Mt. Ophir.

Dermacentor compactus Neumann

Collections from sweeping forest vegetation and from hosts (examined/infested) are as follows:

Sus scrofa (2/2), 800 and 1400 ft, 11♂, 5♀
Vegetation, 500 to 2500 ft, 45♂, 56♀
Vegetation, 2600 to 5200 ft, 1♀

For comments on these collections, see text on *Dermacentor auratus* group and *D. atrosignatus*, and also Tables 1–3.

Amblyomma testudinarium Koch

Collections from sweeping forest vegetation and from hosts (examined/infested) at various altitudes are as follows:

Sus scrofa (2/1), 800 ft, 1 nmyph
Man (biting), 2500 ft, 1 nymph
Man (crawling on), 700 and 1500 ft, 1♂, 2♀
Vegetation, 500 to 2500 ft, 25♂, 20♀, 2 nymphs
Vegetation, 2600 to 5200 ft, 5♂, 3♀, 1 nymph

A. testudinarium occurs practically everywhere in Malayan forests, though usually only in moderate numbers. The incidence on Gunong Benom is either lower than in most other forests of Malaya or collections were made here at periods when adults and other stages were relatively inactive. Forty-seven specimens were taken from vegetation up to 2500 ft, and 9 at higher altitudes.

Only 1 nymph was found on the 2 *Sus scrofa* examined. *Sus scrofa* is the chief host of adult *A. testudinarium* in Malaya and elsewhere in Asia. The incidence of infestation of Malayan wild pigs is usually almost as high as that of *Dermacentor* ticks but the numbers of adult *A. testudinarium* on each pig are almost invariably much lower (unpublished).

Other hosts of adults in Malaya are the tapir, tiger, sambar deer, pangolin, and domestic buffalo. We have records of 5 males, 5 females, and 1 nymph parasitizing human beings in Malaya. Adults also feed occasionally on the tortoise, *Testudo emys*, monitor lizard, *Varanus salvator*, and python, *Python reticulatus*, in Malaya (unpublished).

Immature *A. testudinarium* are the most catholic in host preference of all Malayan ticks. They often occur on domestic chickens, goats, dogs, sheep, and buffalo. While no larvae are recorded from human beings by the Malayan Tick Survey, these tiny ticks are easily overlooked and we suspect that infestation of people may be fairly frequent. A nymph was taken biting a person at 2500 ft.on Gunong Benom. The Hooper Foundation group working with the Gunong Benom Expedition experienced heavy infestation of several members by seed ticks (larvae), presumably *A. testudinarium*, at 3000 to 4000 ft during the wet March-April period but not during the dry month of February (N. J. Marchette, personal communication). Other Malayan hosts of immature stages are (INSECTIVORA), the common treeshrew (*Tupaia glis*); (CARNIVORA), the Malay bear (*Helarctos malayanus*), weasel (*Mustela nudipes*), Malay civet (*Viverra tangalunga*), common palm civet (*Paradoxurus hermaphroditus*) (frequent), small-toothed palm civet (*Arctogalidia trivirgata*), banded palm civet (*Hemigalus derbyanus*), tiger (*Panthera tigris*), leopard cat (*Felis bengalensis*) (frequent), black giant squirrel (*Ratufa bicolor*), three-striped ground squirrel (*Lariscus insignis*), common porcupine (*Hystrix brachyura*) (frequent), wild pig (*Sus scrofa*) (infrequent), mouse-deer (*Tragulus javanicus*) (frequent), cobra (*Naja naja*), monitor lizard (*Varanus salvator*), jungle fowl (*Gallus gallus*) (frequent), and crested green wood-partridge or roulroul (*Rollulus roulroul*). Aside from immature stage hosts reported from Vietnam (Hoogstraal et al., 1968), these are almost the only records of immature-stage *A. testudinarium.*

Engorged *A. testudinarium* reach the largest size (25 × 20 mm) of any tick species in Malaya and a single female may deposit 10,500 eggs. One of us (M. N.) has collected several hundred larvae from forest vegetation a few inches to 3 meters above the ground in the vicinity of a pig wallow in Malaya. In view of the height to which questing larvae climb on plants, it is suprising that this stage is so seldom represented in tick collections from Malayan forest vegetation.

A. testudinarium inhabits forests from Ceylon and India to Borneo, Indonesia, Thailand, Vietnam, the Philippines, Taiwan, and southern islands of Japan. It has not been associated with diseases of man and lower animals.

Amblyomma geoemydae (Cantor)

Six ornate nymphs were collected from lowland forest vegetation and 1 ornate nymph from a coucal, *Centropus sinensis*, at 1000 ft.

A. geomydae parasitizes chiefly reptiles, especially tortoises, *Testudo emys*, *T.* spp., and monitor lizards, *Varanus* spp., in Borneo, Java, Malaya, and the Philippines. Taxonomic problems concerning this species were discussed by Kohls (1957). Disease relationships have not yet been studied.

Amblyomma spp.

Unidentified *Amblyomma* specimens from Gunong Benom are 1 larva from *Echinosorex gymnurus*, 1 larva from *Rattus bowersii*, 1 nymph from *Centropus sinensis*, and 1 nymph from *Anthracoceros malayanus.*

DISCUSSION AND CONCLUSIONS

Ticks from sweeping vegetation

Sweeping (flagging) yielded 546 ticks in lowland forests, 416 in mountain forests, and none in mountain mossy forests (Table 1). Of 5 tick species usually taken in greatest numbers by sweeping vegetation in Malayan forests [*Dermacentor atrosignatus*, *D. compactus*, *Haemaphysalis nadchatrami*, *H. semermis*, and *Amblyomma testudinarium*], each is represented in varying proportions in both altitudinal regions in which ticks were found. The reduction in numbers of *D. compactus* from 16% in lowland collections to 0·24% in mountain forests, was compensated in these zones by a rise in *H. nadchatrami* numbers, from 6% to 54%. As usual in collections from Malayan forest vegetation, *D. atrosignatus* comprised at least 40% of the specimens. No *Dermacentor* were found above 4000 ft. Only *H. nadchatrami* and *H. semermis* were taken in the 4000 to 5200 ft range and, as already stated, no ticks were found above the latter level.

H. c. cornigera adults and nymphs were also collected from lowland vegetation. Reasons for the apparently erratic distribution of *cornigera* in Malayan forests are not known. The collection of nymphs of *A. geomydae* from vegetation is unusual in our experience. The presence of 2 exceptionally rare species, *H. hylobatis* and *H. calvus*, among ticks from vegetation is notable. Reasons for the paucity of *H. koningsbergeri* in collections from Malayan forest vegetation, in areas where this species is believed to be relatively common on small carnivores, remain to be investigated. *Ixodes granulatus*, a medically important parasite of small, ground-feeding animals, is unrepresented in tick samples from forest vegetation; it is a nidicolous species that rarely if ever quests from vegetation.

Ticks from vertebrate hosts

Almost all vertebrates examined for ticks on Gunong Benom were in lowland forests (Table 2).

Bats of the genera *Penthetor* and *Rhinolophus* were infested by larvae, nymphs, and females of *Ixodes simplex*, which has not previously been recorded from Malaya.

The single insectivore, a moonrat, carried *I. granulatus* adults and immature stages, and an *Amblyomma* larva.

Certain rodents yielded a few larvae and nymphs of *H. nadchatrami*, *H. semermis*, *H. koningsbergeri* (tentative identification), *D. atrosignatus*, *D.* sp., and *Amblyomma* sp., and adults of *I. granulatus*. Many rodents were not tick-infested at the time of examination (see footnote, Table 2). The feeding period length of many tropical forest larvae and nymphs should be studied in detail to determine whether comparative rarity of finding these stages on small mammals may be explained by rapid feeding and early dropping from the host.

Each of the 5 wild carnivore species examined was parasitized by adults of *H. koningsbergeri;* a leopard cat was also infested by adults of *H. asiatica* and *H. semermis*, a binturong by adults of *H. hylobatis* and *H. semermis*, and a banded palm civet by nymphs and larvae of *H. vidua*. Lord Medway's dog yielded adult *H. koningsbergeri* and *H. semermis* and larval *D.* sp. Dogs of aborigine villagers bore adults of *H. koningsbergeri* and adults and nymphs of *H. bispinosa*, a parasite that has been introduced into Malaya and seldom infests wild forest animals in this country.

The common large mouse-deer, *Tragulus javanicus*, was parasitized by nymphs of *D.* sp. and *H. nadchatrami*, adults, nymphs, and a larva of *H. semermis*, and, as usual, by all stages of *H. traguli*. One smaller mouse-deer, *T. napu*, yielded only a single larva of *H. ?nadchatrami* (tentative determination). The comparatively heavy infestation of the 2 wild pigs, *Sus scrofa*, by adults of *D. atrosignatus*, *D. compactus*, *H. nadchatrami*, *H. semermis*, and *A. testudinarium* (in this exceptional case only by a nymph) is typical of Malayan collections from this host.

Six of the 9 birds examined on Gunong Benom were infested by specific bird parasites, *H. doenitzi* and *H. wellingtoni*, and by a few *Amblyomma* nymphs, including 1 of *A. geoemydae*. A more extensive study of bird-tick interrelationships on Gunong Benom would be certain to be rewarding.

Ticks biting human beings in lowland forests were adult *H. nadchatrami* and *H. c. cornigera*, adult and nymphal *H. semermis*, and nymphal *A. testudinarium* and *D. atrosignatus*. Adults of these species (except *H. c. cornigera*) and a nymphal *D. atrosignatus* were also collected while crawling on people. At 6000 ft, an adult *H. nadchatrami* was removed while biting and at 3000 ft an adult *H. hylobatis* was crawling on an expedition member. Numerous larvae, presumably *A. testudinarium*, infested persons working at the 3000 to 4000 ft level in the rainy season but not during the dry month of February.

Medical relationships

Owing to the relatively undisturbed forest environment of Gunong Benom and to the continuity of forest from lowlands to altitudinal zones above those inhabited by most Malayan ticks, this mountain area is eminently suitable for investigating the natural history of "primitive" cycles of tickborne pathogens infecting man and lower animals. Among the tick species found here, *Ixodes granulatus* is the original source of the virus (Russian spring-summer encephalitis complex) causing Langat encephalitis. This virus can be transmitted experimentally by other tick species, a finding/that enhances interest in its more widespread presence in nature (see Hoogstraal, 1966). *I. granulatus*, *Dermacentor* spp., and *Haemaphysalis* spp. [including *H. nadchatrami* and *H. semermis*] have been shown by Marchette (1966) to be involved in the cycles of tick typhus (*Rickettsia* sp.) and Q fever (*Coxiella burneti*) in climax forests of Malaya. Lanjan virus, first recovered from *Dermacentor* sp. from Bukit Lanjan near Kuala Lumpur, has recently been isolated from Malayan *I. granulatus* and *H. semermis* (N. J. Marchette, personal communication). Other tick species that should be studied epidemiologically are *H. bispinosa*, owing to its close association/with domestic animals, *H. koningsbergeri* in relation to *Babesia* infections of carnivores, *H. doenitzi* and *H. wellingtoni* to determine their virus-vector potential among wild and domestic birds, and *H. traguli* in relation to infections in the mouse-deer. The question of virus infections in wild pigs and their chief tick parasites, *D. atrosignatus*, *D. compactus*, *H. nadchatrami*, *H. semermis*, and *A. testudinarium*, should also be investigated.

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M. NADCHATRAM

10. PHTHIRAPTERA (INSECTA) CHEWING AND SUCKING LICE

THERESA CLAY

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THE GUNONG BENOM EXPEDITION 1967

9. A COLLECTION OF CHIGGERS FROM GUNONG BENOM (PROSTIGMATA: TROMBICULIDAE)

By M. NADCHATRAM

THIS report summarizes the trombiculid mites collected on Gunong Benom from 17 February through 8 April 1967. Topography and vegetation are described by Medway (1972a) and Whitmore (1972), and the taxonomy and distribution of hosts by Grandison (1972), Hill (1972) and Medway (1972b).

Although the Institute for Medical Research in the past has made intensive as well as extensive collections of trombiculid mites as part of an investigation of the epidemiology of scrub typhus, this is the first time that these and other ectoparasites have been collected on Gunong Benom. The knowledge of the mite fauna of this isolated mountain adds to the information being gathered for zoogeographical and ecological studies. Furthermore, it will enhance our understanding of the ecological relationships of scrub typhus vectors to topography and vegetation.

Mites of the family Trombiculidae (sub-class Acari) are parasitic only in the larval stage (when they are known as chiggers), yet they are amongst the most abundant, both in numbers and species, of all ectoparasites of mammals. They are soft-bodied and range from 0·2 to 2 mm in length. The post-larval stages, i.e. the nymph and adult, are non-parasitic.

The colour of chiggers ranges from white or yellow to light orange or red. Chiggers are essentially habitat-specific, and their colour is to a great extent dependent on their biotope. They may be separated into two broad ecological groups—ground-surface dwellers and nidicolous species. Ground-surface dwellers include the scrub-itch mites and the vectors of scrub typhus, and are coloured orange to red. Nidicolous species, with a few exceptions, are white to yellow, and represent almost 83 per cent of the 146 species of chiggers known in Malaya. Of these 70 to 80 per cent are cavernicolous in habitat, i.e. live in the ground-burrows of small mammals. Nadchatram (1970) has proposed seven ecological groups for the species of chiggers known in Malaya (Ecological Groups I to VII) on the basis of (a) the colour of the chigger prior to attachment to a host, (b) association of the chiggers with habitat and (c) their association with the favoured hosts. Under each species reported below the appropriate ecological group number is given.

The chiggers of medical importance in Malaya known thus far are of two categories. Those that transmit the agent of scrub typhus are *Leptotrombidium akamushi* (Brumpt) mostly found in grassland, *L. deliense* (Walch) mostly found in plantations, forest and the forest fringe and, probably, *L. arenicola* Traub restricted to seacoast vegetation. The other category of chiggers causes dermatitis in man They are *Eutrombicula wichmanni* (Oudemans), *Blankaartia acuscutellaris* (Walch), and *Schoengastia psorakari* Nadchatram and Gentry.

Out of 177 examined, 87 reptiles, birds and mammals were infested with chiggers. Over 3,000 chigger specimens from animal hosts and from ground-holes were collected, representing 35 species in 14 genera. *L. deliense* was found only in small numbers, but a very closely related species, *L. bodense* (Gunther), was abundant. No other of the medically important species listed above were found, although the genus *Leptotrombidium*, which is the important genus from the viewpoint of epidemiology of scrub typhus, is represented by 5 species. The collection yielded a new species of *Myotrombicula* from *Rhinolophus stheno* (Nadchatram and Lakshumy 1969), and a new record of chiggers for Malaya, *Neoschoengastia solitus* Nadchatram, from *Pitta sordida*.

The infestation data is presented in three parts. The first is a list of chiggers found in Gunong Benom with relevant notes on host and habitat distribution. The second part is a list of the infested animals and the species of chiggers found on them, and the third a list of unattached chiggers found in holes.

OBSERVATIONS

1. Chiggers found on Benom

Audyana thompsoni Womersley, 1954

14 ex 1 *Heterometrus longimanus*, 750 ft. This larval species is not a trombiculid, but belongs to a closely allied family, Trombidiidae; it is often found together with a trombiculid species, *Eltonella eltoni*. Colour pallid. Ecological Group VII.

Odontacarus audyi (Radford, 1946)

Two specimens collected, with *Toritrombidula densipiliata*, from *Pitta caerulea*, 800 ft. Orange chiggers parasitic exclusively on birds and widely distributed in Southeast Asia. Indications are that this species is a ground-surface dweller. Ecological Group I.

Eltonella tweediei Audy, 1956

29 specimens ex 8 *Draco* spp., 750 to 800 ft. Because of concurrent habitat-specificity of host and parasite, this species has never been found on other animals. Often found with *Neoschoengastia riversi*. An arboreal species, bright orange to red. Ecological Group III.

Siseca rara (Walch, 1923)

One ex *Pitta sordida*, 900 ft and 2 ex 1 *Callosciurus caniceps*, 900 ft. This is a common species found on reptiles, birds and mammals, including man (in Sumatra). Unfed larvae were recovered from ground-surface and nests of squirrels. Orange to red. Ecological Groups I and III.

Leptotrombidium bodense (Gunther, 1940)

A very common species in Malayan forests, it is represented in the Gunong Benom collection as follows: 6 ex 1 *Napothera macrodactyla*, 700 ft; 3 ex 1 *Echinosorex gymnurus*, 700 ft; 24 ex 6 *Rattus sabanus*, 700 to 1000 ft; 8 ex 1 *R. muelleri*, 800 ft; 36 ex 1 *R. bowersi*, 800 ft; 6 ex 1 *R. cremoriventer*, 800 ft; 124 ex 4 *R. edwardsi*, 3500 to 4000 ft. Unfed larvae of *L. bodense* have been found on ground-surface and in ground-burrows. Ground-surface chiggers are orange and hole chiggers pallid. Nadchatram & Upham (1966) synonymized *L. langati* Audy & Womersley with *L. bodense*. Ecological Groups I and II.

Leptotrombidium deliense (Walch, 1922)

A well-known vector of scrub typhus, this species is poorly represented in the Gunong Benom collection, as follows: 1 ex 1 *Pitta sordida*, 900 ft; 1 ex 1 *R. sabanus*, 800 ft; 16 ex 1 *R. muelleri*, 800 ft; 13 ex 3 *R. edwardsi*, 3600 to 4000 ft. This species, however, is common in plantations and the forest fringe. It has been recorded frequently from ground-surface, ground-burrows, and occasionally in nests of rats and squirrels on trees. It is believed that *L. deliense* evolved from mites of a sylvatic origin and a cavernicolous habitat. Like *L. bodense*, hole chiggers are pallid and ground-surface dwellers orange. Ecological Groups I and II.

Leptotrombidium gentryi Nadchatram & Upham, 1966

This species was first described from unfed larvae collected in ground-holes. The Gunong Benom collection includes 2 specimens collected on a 'bakelite' plate in two separate ground-burrows in a bank alongside a disused logging track, 2½ ft above the ground, at 1000 ft. The host is still unknown. Pallid. Ecological Group II.

Leptotrombidium kundini Nadchatram & Upham, 1966

This species was also taken by plate collections. 13 specimens found in 4 ground-burrows in the bank of the logging track at 1000 to 1200 ft. A pallid species, in Ecological Group II.

Leptotrombidium sylvestre (Audy & Traub, 1950)

39 specimens ex 3 *R. edwardsi*, 3500 to 4000 ft. This is also an uncommon sylvatic species and appears to be associated more with *R. edwardsi* than other rodent hosts. This collection further confirms that *L. sylvestre* is a denizen of montane and sub-montane forests. Pallid chiggers in Ecological Group II.

Toritrombicula densipiliata (Walch, 1922)

12 ex 1 *Pitta caerulea*, 800 ft; 1 ex *Pitta sordida*, 900 ft; and 3 ex 1 *Philentoma velata*, 1800 ft. This species is restricted to birds and widely distributed throughout Southeast Asia, possibly as a result of the migratory habit of some of its hosts (including *P. sordida*). Orange chiggers in Ecological Group I.

Myotrombicula medwayi Nadchatram & Lakshumy, 1969

Gunong Benom is the type locality for this species. A single specimen ex *Rhinolophus stheno*, 700 ft. It is only the second species of the genus known in Malaya. Orange chiggers in Ecological Group V.

Chiroptella sandoshami Nadchatram, 1966

23 ex 15 *Rhinolophus stheno*, 700 to 3600 ft; one ex *R. affinis*, 2500 ft; 2 ex 1 *R. macrotis*, 750 ft. The 24 species of chiggers known from bats in Malaya are apparently exclusive to these mammals. Whether species of chiggers are specific to any species or genus of bats is not yet clear. *C. sandoshami* is a common parasite of *Rhinolophus*, but the apparent host-specificity may be due to ecological factors. Yellow chiggers in Ecological Group V.

Neoschoengastia riversi Wharton & Hardcastle, 1946

18 ex 1 *Draco* sp., 800 ft. Members of the genus *Neoschoengastia* are mostly parasites of birds. In Malaya, however, *N. riversi* is frequently found on flying lizards, although the type host of the species is a bird. Orange chiggers in Ecological Group III.

Neoschoengastia solitus Nadchatram, 1967

4 ex 1 *P. sordida*, 900 ft. This is the first record of its occurrence in Malaya. The host is a migratory bird*. Orange chiggers in Ecological Group IV.

Walchiella impar (Gunther, 1939)

50 ex 1 *Echinosorex gymnurus*, 700 ft; 16 ex 1 *Tupaia minor*, 700 ft; 20 ex 1 *Ptilocercus lowii*, 1700 ft; and 5 ex 1 *R. edwardsi*, 4000 ft. This species is closely related to *W. oudemansi*, but restricted in habitat. Pallid chiggers in Ecological Group II.

Walchiella lacunosa (Gater, 1932)

149 ex 4 *R. edwardsi*, 3500 to 4000 ft. This is a sub-montane species commonly parasitizing *R. edwardsi*. Yellow chiggers in Ecological Group II.

Walchiella oudemansi (Walch, 1923)

2 ex 1 *E. gymnurus*, 700 ft; 127 ex 6 *R. sabanus*, 700 to 800 ft; 101 ex 2 *R. muelleri*, 700 to 800 ft; 5 ex 1 *R. bowersi*, 800 ft; 13 ex 1 *Sundasciurus lowii*, 800 ft; 2 ex 2 *Callosciurus notatus*, 1000 ft; 26 ex 2 *Lariscus insignis*, 700 to 800 ft; 122 ex 1

---

*A new species of *Toritrombicula* was described from the same species of host in the Cameron Highlands (Nadchatram, 1967). The species, *Tori. uphami*, was found with *Tori. densipiliata* and *Odon. audyi*. While the two latter species have been found both on migratory and resident birds in Malaya, it would seem that the host of *T. uphami* was a recent arrival in Malaya.

Rhinosciurus laticaudatus, 700 ft; and 2 ex 1 *Hemigalus derbyanus*, 900 ft. This common species was found on a variety of ground-dwelling and, to a lesser degree, tree-dwelling small mammals, and has been found on man in Indonesia. The range of habitat is also broad. Ground-hole chiggers are pallid and ground-surface dwellers orange. Ecological Groups I, II, and III.

Ascoschoengastia audyi (Womersley, 1952)

7 ex 1 *P. lowii*, 1700 ft; 5 ex 2 *R. sabanus*, 700 ft; 42 ex 2 *C. nigrovittatus*, 700 ft; 164 ex 5 *C. notatus*, 700 to 1000 ft; and 10 ex 1 *Iomys horsfieldi*, 800 ft. *R. sabanus* is an unusual host; this chigger is a common arboreal species frequently associated with tree squirrel in forests and plantations. Traub et al, (1950) recovered *Rickettsia tsutsugamushi* from *A. audyi*. Pink to orange. Ecological Group III.

Ascoschoengastia ctenacarus Domrow, 1962

3 ex 1 *I. horsfieldii*, 800 ft. This is an uncommon arboreal species. Orange chiggers. Ecological Group III.

Ascoschoengastia indica (Hirst, 1915)

2 ex 1 *R. edwardsi*, 4000 ft; and 2 ex 1 *C. nigrovittatus*, 800 ft. The rarity of this species in Gunong Benom is expected since it is essentially associated with commensal rats, especially the house rat *Rattus* (*r.*) *diardii*. It has an extensive geographical, ecological and host distribution. Gispon (1950) recovered the infective agent of murine fleaborne typhus, *Rickettsia mooseri*, from *A. indica* collected from *R.* (*r.*) *diardii* and *R. norvegicus* in Indonesia. White to orange chiggers. Ecological Groups I, II and IIII.

Ascoschoengastia roluis (Traub & Audy, 1954)

4 ex 1 *Ptilocercus lowii*, 1700 ft; 4 ex 1 *Iomys horsfieldii*, 800 ft. This is an uncommon species. White chiggers. Ecological Group III.

Helenicula mutabilis (Gater, 1932)

2 ex 1 *Rattus sabanus*, 800 ft; 3 ex 1 *R. muelleri*, 800 ft; 6 ex *R. bowersi*, 800 ft; and 20 ex 1 *Hemigalus derbyanus*, 900 ft. This species is essentially a ground-surface dweller most frequently found in grassland and is therefore presumed to be a secondary parasite of these forest rats. Orange chiggers. Ecological Group I.

Doloisia brachypus (Audy & Nadchatram, 1957)

2 ex 1 *Sundasciurus lowii*, 800 ft. This squirrel is an unusual host for the species. The genus *Doloisia* represented by 10 species in Malaya, is exclusively intranasal and previously known only from murids. Pallid chiggers. Ecological Group II.

Gahrliepia (Gahrliepia) cetrata Gater, 1932

2 ex 2 *R. sabanus*, 900 to 950 ft; 1 ex *R. edwardsi*, 4000 ft. An uncommon, pallid chigger. Ecological Group II.

Gahrliepia (Gahrliepia) fletcheri Gater, 1932

4 ex 1 *R. sabanus*, 800 ft. This is one of the commonest species of *Gahrliepia* in the Malayan forests. Its replacement by *G. neteralla*, a very closely related species, in Gunong Benom is interesting. Pallid chiggers. Ecological Group II.

Gahrliepia (Gahrliepia) insigne Womersley, 1952

A single specimen ex *R. sabanus*, 700 ft. Yellow chiggers. Ecological Group II.

Gahrliepia (Gahrliepia) neteralla Traub & Morrow, 1955

1 ex *Ptilocercus lowii*, 1700 ft; and 644 ex 23 *Rattus sabanus*, 700 to 1500 ft. This is the second commonest chigger species taken on Gunong Benom. The distribution of this species is spotty, with localized dense populations in some areas, few or none in other. Our records show a similar dense infestation pattern in the Ampang Forest Reserve, Selangor, where the common host was also *R. sabanus*. In most other areas investigated, although *R. sabanus* was caught frequently, *G. neteralla* was either absent or occurred in fewer numbers. Pallid chiggers. Ecological Group II.

Gahrliepia (Gahrliepia) picta Traub & Morrow, 1955

1 ex *R. sabanus*, 950 ft; 1 ex *R. bowersi*, 800 ft. This is a rare species. Unfed larvae were recovered from ground-burrows elsewhere. Pallid chiggers. Ecological Group II.

Gahrliepia (Gahrliepia) rutila Gater, 1932

9 ex 2 *R. sabanus*, 700 to 1000 ft; 4 ex 1 *R. edwardsi*, 4000 ft. This is a rare species; unfed larvae are known from ground-burrows. Pallid chiggers. Ecological Group II.

Gahrliepia (Gahrliepia) sp.

9 ex 6 *R. sabanus*, 700 to 1000 ft. This indeterminate species is intermediate between *G. fletcheri* and *G. neteralla*. Pallid chiggers. Ecological Group II.

Gahrliepia (Schoengastiella) argalea Traub & Morrow, 1957

A single unfed specimen recovered from ground-burrow in the bank of the old logging track, 900 ft. The favoured host of this species is *R. sabanus*. Pallid chiggers. Ecological Group II.

Gahrliepia (Walchia) alpestris Traub & Morrow, 1957

A single specimen ex *Ptilocercus lowii*, 1700 ft. A rare species. Pallid chiggers. Ecological Group II.

Gahrliepia (Walchia) disparunguis pingue (Gater, 1932)

66 ex 2 *Rattus whiteheadi*, 800 ft; 36 ex 1 *Rattus inas*, 3600 ft; and 13 ex 1 *Rattus tiomanicus*, 3600 ft. *R. whiteheadi* is the favoured host of this species. Pallid chiggers. Ecological Group II.

Gahrliepia (Walchia) rustica Gater, 1932

14 ex 2 *R. sabanus*, 800 ft; 156 ex 14 ground-burrows in bank of forest path. Pallid chiggers. Ecological Group II.

Gahrliepia (Walchia) turmalis Gater, 1932

2 ex 1 *Echinosorex gymnurus*, 700 ft; 831 ex 20 *Rattus sabanus*, 700 to 1500 ft; 46 ex 1 *R. bowersi*, 800 ft; 6 ex 1 *R. edwardsi*, 4000 ft; and 5 ex 1 ground-burrow in bank of forest path. This species is close to *G. rustica*, and the commonest species taken in Gunong Benom. Pallid chiggers. Ecological Group II.

2. Hosts

List of numbers infested (number examined in parentheses) and species of chiggers.

REPTILES

Draco spp. 8 infested (of 16): *Eltonella tweediei, Neoschoengastia riversi*

BIRDS

Pitta caerulea 1 (1): *Odontacarus audyi, Toritrombicula densipiliata*
Pitta sordida 1 (1): *Leptotrombidium deliense, Tori. densipiliata, Siseca rara, Neoschoengastia solitus*
Napothera macrodactyla 1 (1): *L. bodense*
Philentoma velata 1 (1): *Tori. densipiliata*

MAMMALS

Echinosorex gymnurus 1 (1): *L. bodense, Walchiella impar, W. oudemansi, Gahrliepia* (*Walchia*) *turmalis*
Rhinolophus stheno 16 (54): *Myotrombicula medwayi, Chiroptella sandoshami*
Rhinolophus affinis 1 (21): *C. sandoshami*
Rhinolophus macrotis 1 (1): *C. sandoshami*
Tupaia minor 1 (1): *W. oudemansi*
Ptilocercus lowii 1 (1): *Ascoschoengastia audyi, A. roluis, W. impar, G.* (*W.*) *alpestris*

Rattus sabanus 24 (33): *L. deliense, L. bodense, A. audyi, W. oudemansi, Helenicula mutabilis, G. (W,) rustica, G. (W.) turmalis, G. (G.) cetrata, G. (G.) insigne, G. (G.) neteralla, G. (G.) picta, G. (G.) rutila, G. (G.) fletcheri, G. (G.) sp.*

Rattus muelleri 2 (3): *L. deliense, L. bodense, W. oudemansi, H. mutabilis*

Rattus whiteheadi 2 (5): *G. (W.) disparunguis pingue*

Rattus bowersii 2 (2): *L. deliense, W. oudemansi, H. mutabilis, G. (W.) turmalis, G. (G.) picta*

Rattus cremoriventer 1 (2): *L. bodense*

Rattus edwardsi 4 (4): *L. deliense, L. bodense, L. sylvestre, A. indica, W. impar, W. oudemansi, G. (W.) turmalis, G. (G). cetrata, G. (G.) rutila*

Rattus inas 1 (2): *G. (W.) disparunguis pingue*

Sundasciurus lowii 2 (4): *W. oudemansi, Doloisia brachypus*

Callosciurus nigrovittaus 2 (6): *A. audyi, A. indica*

Callosciurus notatus 5 (5): *A. audyi, W. oudemansi*

Callosciurus caniceps 1 (1): *Siscea rara*

Lariscus insignis 2 (3): *W. oudemansi*

Rhinosciurus laticaudatus 1 (3): *W. oudemansi*

Iomys horsfieldii 1 (3): *A. audyi, A. ctenacarus, A. indica*

Hemigalus derbyanus 1 (1): *W. oudemansi, H. mutabilis*

Tragulus javanicus 1 (1): *L. bodense*

Heterometrus longimanus 1 (1): *Audyana thompsoni*

3. Unattached chiggers

Aside from the examination of animals for chiggers and other ectoparasites, ground-holes, shallow cavities in the ground, depression under over-hanging roots, and leaf-litter on the forest floor were examined with the aid of strips or plates of black 'bakelite'. Chiggers were found only in tunnels which are presumed to be rat-burrows. Of approximately 40 holes sampled 16 were positive for chiggers, which were represented by the following four species: *Leptotrombidium gentryi, L. kundini, Gahrliepia (W.) rustica* and *G. (W.) turmalis. G. rustica* was the commonest species of hole chiggers. One of the holes found positive for chiggers also yielded several larvae of the common rodent tick, *Ixodes granulatus.*

DISCUSSION

With 35 species, the chigger fauna recorded from Gunong Benom is considered rich considering the short duration of the survey. While this collection fills a gap in our knowledge of the overall distributional pattern of Malayan chiggers, the material reported above is typical of other forests of the Malayan mainland. The survey supports the ecological findings of the author, and in particular the ecological grouping of Malayan species (Nadchatram, 1970). The forest is the reservoir of parasites and, possibly, infections. The constant environment that the forest provides, plus the microclimatic conditions of the subterranean nests of the host animals—ideal for the existence of forest species—, serve to explain why approximately 80 per cent of the 146 Malayan species are endemic in forest. The ease with which the newly hatched larvae of cavernicolous species attach to the host animal (by dropping from the roof of the burrow) is perhaps one of the major contributing factors for the vigorous propagation of the trombiculid fauna.

Several species, i.e. 17 percent of 146 species, proven to be adaptable to fluctuating environmental conditions, are believed to have evolved from a sylvatic origin and perhaps a cavernicolous habitat. These species are found on ground-surface, stems of grass, and leaf-litter on forest floor, and include all species which have been indicted with causing scrub-typhus and scrub itch. Because of the habitats they occupy, these are the species which have the best opportunities of coming into contact with man (Ecological Group I). The writer's observations support the well-known belief that scrub typhus is a man-made malady. When the forest environment is disturbed by man, artificial environments are created which disrupt the natural conditions in which chiggers occur. Some sylvatic species are unable to tolerate the artificial conditions and perish; some that have the opportunity withdraw to their natural retreats, while a few others become adapted to the new situation created by deforestation and flourish. In this new ecological situation other groups of hosts are also encouraged, i.e. ground birds, reptiles, and mammals. Some chigger species, including *Leptotrombidium deliense* the well-known vector of scrub typhus, are readily dispersed by birds and rats. *Rattus tiomanicus jalorensis*, a wide-ranging rat, is a common host of *L. deliense* and most numerous in oil-palm, coconut, and rubber plantations. It also has been collected in sub-montane forest and the fringes of primary and secondary forests.

The 35 Gunong Benom species are placed in six ecological groups. The eight species which fall in Ecological Group I were all collected around the base camp between 700 and 900 ft, where the vegetation is mostly secondary as a result of previous logging.

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THE GUNONG BENOM EXPEDITION 1967

10. PHTHIRAPTERA (INSECTA): CHEWING AND SUCKING LICE

By THERESA CLAY

MALLOPHAGA (Chewing lice) were collected from 26 species of birds and Anoplura (Sucking lice) from two species of mammals. Many of the Mallophaga belong to genera (marked with *) parasitic on the Passeriformes which need revising before accurate determinations can be given; this material will be valuable for such revisions.

MALLOPHAGA

PARASITE	HOST
Menoponidae	
Cuculiphilus snodgrassi (Kellogg & Kuwana, 1902)	*Phaenicophaeus diardi.* (BN. 122)
Bucerocolpocephalum degnani Elbel, 1967	*Anorrhinus galeritus* BB. 09
Myrsidea sp.*	*Calyptomena viridis.* BN. 116
	Garrulax erythrocephalus. BN. 372
	Garrulax mitratus BN. 381
	Stachyris leucotis BN. 432
	Heterophasis picaoides BA. 31
	Hypsipetes viridescens BA. 08
Menacanthus sp.*	*Arachnothera magna* BN. 319
Laemobothriidae	
Laemobothrion maximum (Scopoli, 1763)	*Ictinaetus malayensis* BN. 141
Ricinidae	
Ricinus tinctus, Harrison, 1916	*Criniger ochraceus* BN. 457
Philopteridae	
Craspedorrhynchus sp.	*Ictinaetus malayensis* BN. 141
Cuculicola sp.*	*Phaenicophaeus curvirostris* BN. 166
	Phaenicophaeus javanicus BN. 160
Rallicola unguiculatus (Piaget, 1880)	*Centropus sinesis* BN. 170; BNN. 6

Bull. Br. Mus. nat. Hist. (Zool.) 23, 8

MALLOPHAGA (Contd.)

PARASITE	HOST
Philopterus sp.*	*Harpactes diardi.* BN. 452 *Pitta caerulea* BN. 7 *Terpsiphone paradisi* BN. 461 *Rhipidura albicollis* BN. 332, 337 *Hypsipetes flavulus* BN. 397 *Hypsipetes viridescens* BM. 08 *Dicrurus remifer* BN. 299, 303; BA. 50
Sturnidoecus sp. Nymphs only.	*Indicator archipelagus* BB. 05
Brueelia sp.*	*Megalaima henrici* NB. 171 *Megalaima corti* BN. 342, 326 *Pomatorhinus hypoleucos* BA. 40, 20 *Garrulax erythrocephalus* BN. 372; BA. 33 *Garrulax mitratus* BN. 381
Penenirmus sp.*	*Megalaima henrici* BN. 17 *Psolopogon pyrolophus* BA. 37

ANOPLURA

PARASITE	HOST
Neohaematopinus callosciuri Johnson, 1959	*Callosciurus notatus*
Neohaematopinus batuanae Ferris, 1923	*Petaurista petaurista*

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11. NOTES ON ZOOGEOGRAPHY, CONVERGENT EVOLUTION AND TAXONOMY OF FLEAS (SIPHONAPTERA), BASED ON COLLECTIONS FROM GUNONG BENOM AND ELSEWHERE IN SOUTH-EAST ASIA

1. NEW TAXA (PYGIOPSYLLIDAE, PYGIOPSYLLINAE)

R. TRAUB

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I. NEW TAXA (PYGIOPSYLLIDAE, PYGIOPSYLLINAE)

By ROBERT TRAUB

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SYNOPSIS

Stivalius robinsoni (Rothschild, 1905) and its allies constitute the dominant group of fleas infesting squirrels and tupaiids in the forested foothills of much of the "Indo-Malaysian" region ranging from Indo-China (and perhaps eastern India) through Malaya, to Indonesia and the Philippines. The taxon is reviewed and a new genus is proposed and named to encompass the 4 previously known species and 9 new species. Descriptions, diagnoses and detailed illustrations are provided for these 13 species and 4 new subspecies. The members of the *Stivalius ferinus*-group are also discussed and placed in a separate genus, which is named, described and illustrated, along with a new species from North Borneo and some of the species heretofore known. For purposes of comparison, *Stivalius* Jordan & Rothschild, 1922 *s. str.* is redescribed and figured, and a new subspecies of *S. cognatus* Jordan & Rothschild, 1922 is used to illustrate the diagnostic features of the generic level and those for species and subspecies. Notes on the host-relationships and distribution of these fleas are presented, as applicable. Keys to the known species and subspecies are included for all the genera treated.

INTRODUCTION

THE genus *Stivalius* Jordan & Rothschild, 1922 (*s. lat.*) includes some of the most prevalent and characteristic fleas parasitizing rats, squirrels, tupaiids or other small mammals over much of southeastern Asia and the Indo-Australian Archipelago, and hence throughout this vast area *Stivalius s. lat.* must be considered as of potential importance regarding vectorship of any infection harbored by rodents and other such mammals. In fact, species of *Stivalius* have been found infected with plague in India and Java (Pollitzer, 1954), as is pointed out below.

The fleas collected by Lord Medway's team on Gunong Benom in Pahang, Malaya (W. Malaysia) amply indicate the predominance of *Stivalius s. lat.* in the relatively untouched dipterocarp forests of that country, but the value of the collection far exceeds that point, or that of the new species represented therein. The specimens well illustrate certain major points concerning the systematics, zoogeography and evolution of fleas, and contribute to our understanding of the current and past distribution of host-mammals. The findings emphasized the need for the revision of the classification of the *Stivalius robinsoni*-group of fleas, and of certain other members of *Stivalius s. lat.*

For these reasons, it was decided to regard the Medway collections as the foundation and catalyst for a study dealing successively, in three articles, with taxonomy, convergent evolution and zoogeography of certain groups of *Stivalius*. This first paper in the series includes: (1) the erection of a new genus for the *S. robinsoni*-group, with descriptions and illustrations of nine new species and four new subspecies, along with keys for the identification of the 13 known species and four subspecies. The hitherto unknown female of *S. loncha* Jordan, 1926 is described. (2) A discussion of the hosts and distribution of the Malayan peninsular species of the *S. robinsoni*-group. (3) A new genus for the *S. ferinus*-group, with descriptions and figures of one new species and a key to the five known species. (4) A redefinition of *Stivalius s.str.*, for purposes of comparison with the new genera, and based upon a new subspecies of *S. cognatus* Jordan & Rothschild, 1922, along with keys to the described forms (four species and three subspecies), including the hitherto unknown male of *S. c. spiramus* Jordan, 1926. Dorsal or ventral views of the aedeagus are presented to elucidate some of the major points in systematics, comparative morphology or convergent evolution.

The second and third articles in the series follow immediately after this one.

MATERIALS AND METHODS

Methods of Collection and Handling

It is emphasized that throughout the course of the field-projects in Malaya, Borneo, Thailand and other countries, which resulted in the specimens treated in this article, the collectors were primarily engaged in other types of studies. The investigators were actually working on scrub typhus, leptospirosis and other infections, or doing research on land-leeches, or engaged in malaria-control, or conducting survey-type operations, and the small number of specimens of fleas obtained at times, and the limitations of the data on infection-rates, reflect the necessarily secondary nature of the collecting-programs.

The bulk of the specimens were collected by the writer while serving as Commanding Officer of the U.S. Army Medical Research Unit (Malaya) during varying periods in Malaya from 1948 to 1959, or by teams of the Colonial Office Medical Research Unit (later Division of Virus Research and Medical Zoology) of the Institute for Medical Research, under the direction of Dr J. R. Audy. Both of these Units were based on the grounds of the Institute for Medical Research (I.M.R.) at Kuala Lumpur and worked closely together. Other important collections were made by the Department of Zoology, University of Malaya (UM), by teams led by Lord Medway or J. R. Bullock. The U.S. Army Medical Research Unit (USAMRU) required live animals for its research on infections, while the British (later Malaysian) Unit (henceforth indicated as DMZ-IMR) was collecting living animals in connection with studies on ecology. Lord Medway also frequently needed the animals alive for his investigations.

For these reasons the vast majority of rats, tree-shrews and ground-squirrels, and even many tree-squirrels, examined for fleas in Malaya had been trapped in various types of live-traps, predominantly in the "wire basket-trap," a modification of a trap of presumed Chinese origin and commonly used for catching rats throughout southeastern Asia. In this type of device, constructed of thin chicken-wire, the front door is closed by a spring when the mammal tugs at the bait on a hook and thereby releases the mechanism holding the door open. A folding-trap of heavy wire, of U.S. design, was also employed and in this type, the door was released by a treadle on the floor. Closed traps of galvanized metal, operating in a similar way, were also used. Another kind was prepared by fastening a large can to an ordinary large snap-trap and placing a screen on the movable arm of the trap. When released, the arm would hurl the rat into the can and close the aperture.

Sundry modifications of these and other live-traps were employed, but regardless of the model, there were always inherent disadvantages insofar as concerns the collecting of fleas. Certain species tend to leave the host soon after feeding to repletion, others do so when the animal becomes excited, and its fur gets ruffled, as happens when the mammal realizes it is trapped. Since the traps were generally examined but once daily (and the animals became agitated anew at the approach of the collector), many fleas were undoubtedly lost before the host could be popped into a cloth bag for subsequent examination. In traps made of mesh, the mammals would become drenched during showers of heavy rain, which usually are a daily occurrence in or near the tropical rain-forests. In traps of solid metal, the host often became too hot, and hyperactive, or died as a result, while at other times, as at night, they became wet and cold with equally disastrous results. These consequences all affected the degree of flea-infestation at the time of collection, as did the attack on the hosts by myriads of ants, both large and small, which was a fairly frequent occurrence.

On the other hand, utilization of traps which killed the victims, i.e., snap-traps of sundry sizes, or dead-falls, had other and more serious disadvantages, even though some species of fleas linger for hours on a dead host. Within minutes, dead rats almost invariably attracted swarms of ants, whose movements through the fur unquestionably hastened the departure of many fleas. The removal of innumerable chunks of skin by the ants also would effectively depilate the carcass within an hour or two, and only exceedingly rarely was a flea ever noted on the body of an animal infested by ants. Even when the traps were examined every hour it was impossible to cope with the depredations of the ants in some areas. Nevertheless, the use of snap-traps was a useful adjunct, especially in the mountains, and certain "rare" fleas were collected by this means.

The bait used in the trapping operations consisted of fruit such as bananas or durian, burnt coconut, nuts, peanut butter, sweet potato or other yams, dried fish, bacon, a mixture of oatmeal, peanut butter and bacon, etc. Baits that were sweet (e.g., raisins) or oily or fat tended to attract so many ants that they were soon eaten without trace.

Trapping was supplemented by shooting, and most of the tree-squirrels and some of the ground-squirrels and *Tupaia* were collected in this way. Carnivores, in particular, were taken by shooting, usually at night, when their eyes would glow in the light from powerful flashlights.

All hosts, including live animals, were immediately placed in individual cloth bags on collection and the bags were sealed pending examination in the laboratory. The bags of dead specimens were treated with chloroform and sprayed with aerosol insecticide to stupefy or kill the fleas; while live animals destined for release after checking were exposed to ether long enough for anesthesia, whereas those required for microbiological study were chloroformed. (Chloroform is more effective but ether is less toxic, hence the use of the latter.) If living chiggers or other ectoparasites were required for inoculation, rearing or study, the host was asphyxiated after exposure to the anesthetic; the host was then brushed vigorously while it was held over a tray, and the stupefied fleas which fell in the process were collected via forceps and preserved in 70% ethyl alcohol. The brushing was repeated several times because of the difficulty in collecting all the fleas hidden in the fur. The fleas were prepared for definitive examination and study by placing them in 10% KOH for 24–48 hours or until the internal tissues had dissolved, after which they were washed in water, dehydrated by exposure to 70%, 95% and 100% ethyl alcohol in series, cleared in oil of wintergreen and mounted in Canada balsam on microscope-slides.

In the case of mammals collected by USAMRU, records were kept as to the numbers of hosts which were not infested with fleas. This was not possible routinely for the collections by our colleagues, but the difficulties mentioned above in collecting fleas in the tropics serve to demonstrate inherent limitations in obtaining infestation-rates in such regions. When discussing the numbers of fleas taken from various hosts, as in Table 2 (p. 259), the entry "minimum number exam'd." therefore refers only to the mammals collected by USAMRU.

Major Collection Areas

Specimens of fleas of the *S. robinsoni*-group were never taken in fields of grass or waste land, but only where there was forest, at least in remnant form. Accordingly, the major collecting areas on the Malayan peninsula were in the dipterocarp forest in the lowland or foothills, particularly within 20 miles of Kuala Lumpur, i.e., the Forest Reserves at Gombak, Ulu Langat, Bukit Lagong and Kepong, and also at Klang Gates (Selangor), where trees such as *Shorea*, *Dipterocarpus*, *Swintonia* and *Balanocarpus* and *Hopea* dominate the forest. Most of the collections were made between 800 and 2000 ft elevation (mainly at 1500 ft) in areas which were still largely "primary jungle" in 1948–49 but which were thereafter fairly extensively but selectively thinned for timber so that by 1956, bamboos and other features of secondary forest were evident in scattered patches throughout. The findings in the dipterocarp forest are treated below as "Kuala Lumpur Forest" (Table 1, p. 216, et seq.). Another well studied site was the Subang Forest Reserve west of Kuala Lumpur, about 8 miles from Batu Tiga on the Batu Tiga–Subang road. Here the forest was of a much more secondary nature and at a lower elevation (at about 200–600 ft) than in the wooded habitats mentioned above.

Field work was undertaken in the limestone hills west of Ipoh, Perak, as a result of an outbreak of scrub typhus in British forces operating deep in the (secondary) forest. This was in the Kledan Saiong Forest Reserve, 8 miles west of Ipoh and again 10 miles northwest of Ipoh, each trip including about 4–5 days intensive collection at elevations of about 800–1100 ft in September–October 1958. The habitat at Gunong Benom, the scene of operations for Lord Medway's expedition, has been discussed elsewhere in this volume. Limited collections were also made by USAMRU in the coastal or adjacent forests of the East Coast, i.e., at Kuantan, Pahang, and at Bukit Besei in Trengganu. Another area of dense lowland forest briefly examined was that in Kelantan.

Over the years, about one month was spent by USAMRU (and an equivalent period by DMZ-IMR) collecting in the montane forests in the vicinity of Fraser's Hill (3500–4500 ft elev.), the Cameron Highlands (4500–6600 ft), and about 2–3 weeks at Maxwell's Hill (3900–4200 ft) and Kedah Peak (Gunong Hijau, G. Jerai) (3500–3900 ft). These areas, in general, have essentially the same mammalian, siphonapteran and trombiculid fauna and hence the collections are consolidated under the caption "Mountains" in the discussion of host-relationships below (but an exception is noted in the case of Kedah Peak). An interesting set of specimens was taken in Kedah by a group from the Department of Zoology of the University of Malaya (UM) under the direction of J. R. Bullock. This was at the Bukit Wang Forest Reserve at Jibra and the results are treated separately. Other valuable material was collected by UM teams on Tioman Island (Pulau Tioman) off the East Coast of Malaga.

Although three joint teams of USAMRU and DMZ-IMR operated on Mt. Kinabalu, North Borneo (Sabah), based at 5000 ft elevation at Tenompak for periods of about 4–6 weeks annually, in 1951–1953, and Lord Medway's group also collected there subsequently, as have other naturalists interested in ectoparasites, no specimens of the *S. robinsoni*-group have ever been taken at such altitudes (or higher) in Borneo. However, we did find such fleas on flying-squirrels and in squirrel nests, etc., in the vicinity of Ranau, at the base of this mountain, as indicated in the description of a new species below.

Other areas where members of the *S. robinsoni*-group were taken, in Sarawak, Thailand and Indonesia, etc., are indicated, along with the collectors, in the descriptions that follow. The individuals and institutions participating in all of these studies are mentioned in the paragraph on acknowledgements.

Introductory Remarks Concerning the Descriptions

Format and Keys

The *S. robinsoni*-complex of fleas is relatively rich in numbers of species, and some of these are superficially similar in appearance (although differing abundantly in critical details—at least in the males). Moreover, as many as three species have been collected on the same individual ground-squirrel. Accordingly, in order to facilitate identification and to provide an adequate background for the evaluation of differences at the generic-, species- and subspecies-levels and for use in discussions on evolution and zoogeography, the various species are diagnosed and illustrated in detail.

Further, the first new species is described in full so as to serve as the basis for comparison for the forms that follow. Major distinctions alone are therefore stressed in diagnoses, and only significant morphological differences are cited in the descriptions following such analyses. In the keys for identification of species and subspecies, frequently more than one set of diagnostic characters is cited in the couplets. This was done to facilitate the use of the keys, so that if there is indecision about one point, an alternate is available. It is stressed that each feature is diagnostic, i.e., only one need apply, and hence the couplets do not deal with combination of characters, but with alternates.

Landmarks and Points of Reference Used in Taxonomy

The most important features for classifying the members of the *S. robinsoni*-group (and other *Stivalius s. lat.*) are in the male sternum 9 and the aedeagus, and in the internal genitalia of the female, including characters unused or un-noted in the past. These are all labeled and indicated in the text and figured and defined, if new. However, in addition there are morphological structures and "landmarks" that are useful in taxonomy but which are difficult to describe in a few words, or to locate precisely because they are on a curved surface, or else are not oriented in the usual fashion (i.e., the "ventral arm" of the male sternum 9 is often caudal or vertical in position).

For clarification and simplification, therefore, a system of reference-points, utilizing lower case letters, has been employed in some instances (head, claspers, male sternum 8 and sternum 9) to designate the specific level or site being described or compared.

Claspers, Sterna 8 *and* 9. The need for a system of this type becomes apparent by a glance at figs 28 and 29, the male sterna 8 (8 S.) of two allied fleas. It is obvious that the outlines of the sterna differ markedly, and in the case of the former (fig. 28) the temptation is to say the "dorsal margin is flattened." However, a question arises as to the "dorsal margin" in the latter, for what appear to be the anterior and posterior margins curve together imperceptibly. Moreover, study of the cutaneous marking or striae indicates that the dorsal margin really extends down to the first (uppermost) large bristle on the caudal margin.

The structure herein termed the "lumacaudate process" (LUM.), on 8 S., emphasizes the problem, for while there are noteworthy differences in proportion, there are inadequate landmarks to use in comparison. Thus, in the case of fig. 29, the length is fairly easy to determine because the dorsal margin is outlined, but this is not so in the other species.

Accordingly, the following reference-points have been selected as guide-marks. In the case of the claspers and sternum 9, they are illustrated only in figs 1 and 3 which were specially prepared for this purpose, although the abbreviations are frequently used in the text. It will therefore be necessary to refer to these figures, or to the List of Abbreviations (Landmarks and Points of Reference on p. 298) below, in order to properly utilize this system. However, the text has been so prepared that the sundry structures are generally described in the usual manner and hence are self-explanatory, while the reference-points are cited to serve as supplemental guides.

The exceptions are instances used in comparisons, and these immediately follow such descriptive phrases, and therefore should not be confusing.

Chaetotaxy and Dimensions of the Preantennal Region. Members of *Stivalius s. lat.* are liberally endowed with bristles, and the number and shape of the sundry preantennal bristles are often important in taxonomy. Unfortunately, the bristles (except for those in the first row) are usually not arranged in definite rows, unlike some other groups of fleas. Moreover, when relatively large numbers are present, there is some variation in both arrangement and actual number, in accordance with a well known principle in insects. In order to facilitate discussion and indication of the major preantennal bristles, an arbitrary system has been used to designate "rows" of bristles, as shown in fig. 2 (I–IV). No logical pattern could be discerned which would encompass all the large bristles, and the one or more which do not fall in the rowa are indicated as "supernumerary" (SY.). It should be noted that not all the members of "*Stivalius*" have preantennal chaetotaxy that jibes with even this arbitrary system, but at least it is possible in this way to more readily categorize and denote the "exceptions."

In the species illustrated in fig. 2, the bases of the anteriormost row of bristles are linked by a cuticular line and hence this row, designated as I, is unmistakable. The next row, of four subvertical large bristles, is II. The third row, III, distinguished by the eye-bristle (E.B.), which is above and anterior to eye, may be termed the eye-row (E.R.B.). It consists of three sub-horizontal long bristles, and commences in line with the ventralmost of II. Row IV is likewise sub-horizontal and is termed the genal row of bristles (G.R.B.), ranging along ventral margin, from the base of the maxillary lobe (MX.) half-way towards the ventral part of the eye. In addition there is one large bristle out of line, between II and III; it is designated as a supernumerary (SY.).

The shape of the head is likewise of significance in the classification of pygiopsyllids, but here, too, difficulties arise. Not only do the sexes differ (as in other fleas), and there also are the usual problems of indicating unmarked points on curved surfaces, but variations occur in the position of certain "landmarks," depending upon the taxon. Thus, in one new genus herein described, the maximum length of the preantennal region is at the level of the median sensillary crater (fig. 2, M.S.C.), but in another, the crater is more dorsal in position, where the frons is narrower. In some instances the labral or anteroventral angle of the head is in line with eye-bristle, in others, not. Those "lengths" are therefore not comparable. Another problem is that structures that would appear to be useful as landmarks are either movable, and hence subject to individual variability (i.e., the palpi and the maxillary lobe), while others are at times impossible to see clearly (i.e., the bases of the palpi). In order to make valid comparisons, therefore, guide-marks are indicated in fig. 2 as follows:

The *height* of the preantennal regions is measured from the level of the vertex at the falx, viz., j3–i3, to the true ventral margin of the head (f4–g4). The *length* may be measured at various levels, according to genus and sex, but always should be along lines parallel to the longitudinal axis of the flea, and directed to the margin of the antennal groove, i.e.: (1) immediately below the middle sensory crater (M.S.C.)

(x3–y3); (2) the dorsalmost long bristle of row I (z3–a4); (3) *ibid.* for row II (a4–b4); (4) the eye-bristle, which at times is in line with the labral angle and then would be d4–e4; and (5) the most anterior point on the arc of the frontal margin, which in fig. 2 is the same as level b4–c4. Other aspects of this system are cited in the List of Landmarks (p. 298).

A. **Medwayella** gen. nov.

DIAGNOSIS. ♂ instantly recognizable by the ventral spinose "lumacaudate" process on sternum 8 (figs 29, 12, LUM.). Shape and structure of ♂ sternum 9 (figs 1, 18, 20) and of sclerites of aedeagal endchamber (figs 10, 22–25) are characteristic and are described below. Spermatheca (fig. 15, SP.) shaped somewhat like a ground-nut or peanut and with basal portion of duct of spermatheca (figs 15, 27, D.SP.) bearing internal sclerotized rings. ♀ basal sternum with lateral patch of bristles restricted to proximal portion of segment. ♀ tergum 8 bearing a mesal tanned zone (figs 27, 31, M.R.8) anteriorly marked by a vertical ridge and a contiguous dark ovoid area.

GENERIC DESCRIPTION. Caput integrecipit (figs 4, ♂; 6, ♀). Anterior margin of head evenly ovate, upper half more rounded than lower. Front part of ♂ head about thrice as high (from vertex at falx, to ventral margin) as long (at level of dorsalmost bristle of row II, viz., b4–c4 in fig. 2). Preantennal region with 4 irregular rows of bristles, the lowest ventromarginal. Eye reniform, well developed, inserted far back, above base of procoxa. Antennal segment 2 with bristles short in both sexes. Antennal groove not extending on to propleuron. Postantennal region with 3 complete rows of bristles. Labial palp (L.P.) 5-segmented (excluding palpiger) and generally reaching near apex of procoxa; occasionally longer (fig. 104).

Prosternosome lacking distinct sinus for receiving first vinculum (VC.1.). Dorsal margin of pronotum subequal to, or slightly longer than, length of adjacent spines of comb. Mesonotum (fig. 9, MSN.) generally with 1 pseudoseta (PS.S.); subdorsal. Pleural arch (figs 6, 9, PL.A.) well developed. Metanotum (MTN.) lacking apical spinelets. Metacoxa lacking mesal spiniforms, but with a few mesal thin bristles. Profemur lacking a group of mesal bristles but with scattered lateral ones. Meso- and metafemora lacking median and submedian lateral bristles. Dorsolateral bristles in notches on posterior (outer) margin of tibiae largely paired. First metatarsal segment about 1·6 times length of II and nearly 2·5 times that of mesotarsus I. Third metatarsal segment longer than fifth. Except for fringe on first segment of protarsus, none of tarsal bristles extending well beyond middle of following segment. Tarsal segment V with 6 pairs of stout lateral plantar bristles, of which first pair displaced towards midline on pro- and mesotarsi (fig. 7), and third pair somewhat so displaced on all legs (fig. 8, metatarsus). Fourth vinculum (fig. 9, VC.4) usually upright and not projecting forward as a short rod. Some abdominal terga with 1 subdorsal apical spinelet. Unmodified terga very broad, extending ventrad to lower third or fourth of sterna; with 2 virtually complete rows of bristles in ♂, 3 in ♀ but incomplete. Basal abdominal sternum of ♀ with lateral patch of small bristles, but these near anterior margin; nude in ♂. Fossae of representative abdominal spiracles sagittate. Both sexes with 2 antepygidial bristles per side (figs. 11, ♂;

26, ♀, A.B.). Tergum 7 of ♀ with some bristles modified to resemble antepygidials, i.e., 1 dorsomarginal (U.M.B.), one immediately below plate of A.B. (L.M.B.) and 1 (L.B.M.-2) in ventrocaudal corner of group of bristles of 7 T. Tergum 7 produced into a short lobe (U.L.7) above A.B. plate and, in ♀, a longer, pointed lobe (L.L.7) immediately below it. Sensilium (pygidium) higher than long in ♂ (figs 11, 13, SN.); not as arched in ♀, where dorsal-ventral axis slightly exceeds anterior-posterior axis (fig. 26, SN.).

Male. Tergum 8 (fig. 11, 8 T.) very small, extending only slightly ventrocaudad of its spiracular fossa (8 SPC.). Sternum 8 (8 S. and fig. 28) correspondingly very large, extending dorsad to near base of ventral anal lobe (V.A.L.) and cephalad to about level of A.B.; "lumacaudate" in bearing a conspicuous, spinose, mesal ventral bulbous process (LUM. and fig. 12) arising near middle of ventral margin. "Lumacaudate process" attached to 8 S. by an apical fold or seam (S.LUM.); inner surface armed with close-set spiniforms from near basal fourth or fifth, to apex; spiniforms directed mesad. Ventral anal lobe (fig. 13, V.A.L.) with ventral margin with a conical process at middle; this bearing 1 long apical bristle, hence structure somewhat resembling anal stylet of ♀ (fig. 27, A.S.). Subanal sclerite (S.S.) relatively large and well tanned. Manubrium (MB.) broad to near apex; ventral margin with apical third quite straight but usually biconvex near middle; dorsal margin somewhat convex; its bay (B.MB.) extending cephalad to near apex. Immovable process of clasper (figs 14, 17, P.) dorsally somewhat truncate except for caudomarginal bulge around longish apical bristle; with a smaller dorsal bristle. Conical process (C.P.) of P. usually more than 5 times as long (cf. fig. 1, e–h)[1] as broad at middle (f–g). Movable finger (F.) of clasper with stiva (STV.) (distocaudal extension) too short to resemble a plough-handle and base far too broad to look like a plough-shaft (in contrast to the condition in *Stivalius s. str.*, which suggested to Jordan the coining of the generic name based upon the Latin word, *stiva*, for plough-handle). Caudal margin of F. usually sigmoid so that F. is narrowed subapically and bulges caudad proximally. Distal fringe (D.FR.) generally of about 4 stout bristles; subapical, at level of sensilla-group (S.G.) of 3 short bristles; the bases of bristles of the fringe mesal and slightly anterior to caudal margin of F. (vide fig. 87). Fulcral sclerite (F.S. and fig. 65) of F. about 1·3 times as long (high) (fig. 1, ww/xx–zz/a3) as broad at expanded base (ww–xx). Tergal apodeme of segment 9 (T.A.P.9) long and narrow. Proximal arm of sternum 9 (P.A.9 and fig. 63) apically massive, and base rapidly broadening so that subapical breadth (cc–ee) is about 2·5 times that of base (gg–hh).

Distal arm of sternum 9 (figs 18, 20, D.A.9) subequal to P.A.9 in length (fig. 1, ii–qq; ii–arc aa/bb) and characterized as follows: (1) Fairly long and narrow, somewhat broadening at level of transverse sclerotization (T.S.) which represents dorsal limit of internal fusion of the two distal arms. (2) With subapical group of 4–6 caudomarginal (ventromarginal) short spiniforms (S.G.SPN.). (3) Caudomarginal submedian group of 2–3 stout bristles (CM.G.B.) above T.S. (4) A median dense group of microspinules in clear area near tip of D.A. 9 herein termed the subapical patch of microspinules (MSP.P.) and presumably sensory in function. (5) With subapical lobate extension (SUB.L.) on anterior (dorsal) margin; this bearing a group of fine bristles near margin. (6) Often with a distinct subapical dorsal (anterior) notch (fig. 20, NCH.) or broad sinus (fig. 33, ARC.) resulting in a characteristic apical lobe (AP.L.). If sinus or arc absent, then margin between apex and SUB.L. quite homolate ("uniform-sided," viz., flat and unmodified) (fig. 67, HOM.). (7) With a laterad-directed, lightly tanned, flap herein termed the supramedial flap (SUP.FL.) overlapping more mesal patch of microspinules (MSP.P.); its basal margin extending from near level of SUB.L. to, or near, apex of D.A.9, its ventral (caudal) margin delineated by a median arc of thin bristles, the supramedial group (SUP.G.). Base of SUP.FL. associated with a sclerotized thickening (THK.), at least for upper portion. (SUP.FL. appressed to surface of D.A.9 in mounted specimens and hence appearing as contiguous with it and not at all flap-like.) (8) With a convex semimembranous microtufted or microspiculose area in a cavity of anterior (dorsal) margin at level of T.S. herein named the mid-microspiculate area (M.MSP.), and of presumed sensory function. (9) In some species, heavily sclerotized and ventral margin appearing as an apical spur-like extension (fig. 111, EXT.9) because of semimembranous nature of distal portion of dorsal margin.

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[1] For methods used in measurements, see figs 1–3 and text pp. 209–211. The small letters indicate the points in question; letters connected by a dash denote the two points or axes being measured, while a fraction signifies an imaginary line connecting those points. Thus, ww/xx–zz denotes the distance between zz and an imaginary line connecting ww and xx.

Aedeagal apodeme (fig. 10, AE.A.) resembling manubrium (MB.) for most of its length; lacking apical appendage. Middle lamina (M.LAM.) with its bay (B.M.L.) extending nearly as far cephalad as anterior margin of bay of manubrium (B.MB.) when the two apices are contiguous. With an ovoid, subdorsal cavity in lateral laminae containing a spiculose body, the entire structure herein termed the caverna spiculosa (fig. 22, CAV.SPIC.). Aedeagal pouch (AE.P.) well tanned; thickened ventral walls (figs 23, 42, AE.P.-V.) extending cephalad to level of F.S. and distad to level of base of sclerotized inner tube (S.I.T.), near base of phylax (PHY.); lateral walls (AE.P.-L.) continuing along sides of the crochet process (CR.P.) and blending with it, appearing at least as the basal ventral portion of the "crochet" (fig. 22) and at times as the entire ventral part (fig. 71); the unified structure, whose components are at times difficult to delimit, herein termed the quasi-crochet (Q.C.). Hood (HD.) sinuate to ventral margin and then projecting anterodorsad as the lateral "deltoid flap" (DEL.FL.), which covers much of the endchamber except for base of phylax (PHY.) and base of S.I.T. Deltoid flap dorsocaudally terminating at dorsal apex of body of crochet (B.CR.); its own apex subdorsal, at level of aedeagal fulcrum (AE.F.). Lateral lobes (L.L.) reduced; primarily ventral in position and mesad of DEL.FL.; extending from apex of thickened ventral margin of pouch wall over base of phylax of crochet process and here merging with caudolateral region of pouch wall (AE.P.-L.). Sclerotized inner tube (S.I.T.) relatively unmodified, fairly long, horizontal and sinuate and with ventral margin extending somewhat more distad than dorsal margin; distal third ridged, often with a dorsal spur-like projection (figs 23, 96). Ford's sclerite (F.SC.) (formerly termed apicomedian sclerite) very well developed; apex of its alpha-portion (ALPH.) thumb-like (THM.) or else forming a groove-like structure (figs 71, 115, GRV.) by paralleling part of the thickened basal margin of the securifer (SEC.). Upper arm (U.A.) of securifer narrowed distally; lower arm (L.A.) broad to at least middle and then narrowing somewhat. Ford's sclerite bifid to midline in dorsal or ventral aspect (figs 24, 25). Phylax (PHY.) relatively broad (lateral aspect); about twice as high as broad at base; subligulate, with ventral margin straight; arising near apex of pouch wall at fusion with lateral lobe (L.L.) and extending to apex of pivotal ridge (PIV.R.) of aedeagus. With a short, tanned "pivotal chord" (PIV.CD.) linking apicocaudal angle of PHY. with base of U.A., arising at apex of PIV.R. Crochet boomerang-shaped, its body or basal sclerite (B.CR.) vertical, narrow except for expanded truncate apex which is contiguous with base of Ford's sclerite (F.SC.) and junction with DEL.FL.; crochet process (CR.P.) extending caudad as a horizontal digitoid arm and ventrally indistinguishably fused with AE.P.-L. to form the quasi-crochet (Q.C.). Often with a semimembranous spiculose lobe (fig. 22, SPIC.L.) (which is probably the ventral lamella of Hopkins & Rothschild 1966), apparently arising from base of phylax and intimately associated with ventral region of Q.C. Aedeagal fulcrum (AE.F.) quite narrow. Crescent sclerite (C.S.) long. Satellite sclerite (SAT.S.) very short. Central sclerite (CEN.S.) very close to fulcral medial lobe (FUL.M.L.), the two together resembling upper portion of an arrow-head. Lateral shafts of capsule (L.S.C.) well tanned. Y-sclerite (Y.S.) large. Vesicle (V.) well developed. Penis rods (P.R.) short and thick. Third apodemal rod (AP.R.) of endophallus nearly as long and stout as penis rods.

FEMALE. Spermatheca (fig. 27, SP., and fig. 15) with bulga (B.) about twice as long as broad, medially somewhat constricted dorsally and with basal (caudal) part of bulga slightly broader than apical; hilla (H.) short, basal portion internal and entire length only slightly exceeding maximum girth of bulga; with an apical papilla (PAP.). Duct of spermatheca (D.SP.) with portion near bursa copulatrix greatly dilated (figs 27, 77, DIL.P.) and with long internal slightly sclerotized annulae; middle portion narrower and bearing a ladder-like series of internal sclerotic rings; portion nearest spermatheca still narrower and also with dark annulae. Blind duct of bursa copulatrix inapparent. Bursa copulatrix (B.C.) with its perula (P.B.C.) somewhat ovate (fig. 31) or broadly vermiform (fig. 77). With a large sac (SAC.) associated with DIL.P. and dorsal region of perula. Duct of bursa copulatrix (D.B.C.) lightly tanned and sinuate (degree depending upon relative position). Lura of bursa copulatrix not specialized. With an accessory "gland"[2] or fissure anterior to glandula vaginalis (G.VG.) and at times, one caudad. With a paired, internal, semimembranous structure lying between bursa copulatrix and ventral part of sternum 9 (9 S.), immediately above G.VG. and caudoventrally associated with dorsal wall of vagina at genital chamber, and herein termed the paragenital morion (PG.M.). When well developed, PG.M. occupies most of this space (i.e., fig. 77) but it may be greatly reduced (fig. 31). It is of unknown homology and function but may have something to do with the muscles controlling the vaginal aperture and/or with the bursa copulatrix. Sternum 7 (7 S.) with a ventral lobe. Ventral anal lobe (figs 16, 27, 73, V.A.L.) with base short; apical margin long and sinuate, with spaces between groups of long bristles. Dorsal anal lobe (D.A.L.) with 1 long bristle above, and another immediately below base of anal stylet (A.S.), which is quite straight, long and narrow. Tergum 8 (fig. 26, 8 T.) with caudal margin bearing a long, shallow sinus extending from near apex to lower fourth; usually with a protruding lobe at ventrocaudal angle; with a pair of mesal, long, thin marginal setae above lobe and another pair of such genitalic bristles at level of V.A.L. With mesal tanned genitalic ridge (M.R. 8) marked by anterior, often sinuate or crescentic, vertical thickening, the dorsal or median portion of which is buttressed by a small ovoid sclerotized area. Eighth spiracular fossa (8 SPC.) relatively small, vertical portion ovate, about twice as high as long. Sternum 8 (figs 27, 32, 8 S.) flask-shaped, with dorsoapical short bristles.

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[2] These "glands," like the glandula vaginalis and duplicatura vaginalis, presumably house various hooks or lobes of the male in copulation, and are probably not glands in the usual sense of the word, although they may be lined with cells that provide lubrication, etc.

The type of the genus is *M. dryadosa* sp. nov. described and figured below. Here also belong the members of the "*Stivalius robinsoni*-group" of Smit (1958), viz., *robinsoni* (Rothschild, 1905), *rhaebus* Jordan, 1926, *lonchus* Jordan, 1926, *javanus* Jordan, 1933 (to use the original spelling, instead of the feminine endings, as henceforth) and the additional new species described below.

Comment. The genus is named for Lord Medway, both for the present holder of the title and for the former, now the Earl of Cranbrook, in token recognition of the many contributions these scientists have made to the study of the natural history of mammals and birds in the Indo-Malaysian area. It is also pertinent and significant that the Earl of Cranbrook's collections of insectivores in remote regions of northeast Burma and those of his son Gathorne, the current Lord Medway, in Malaya and Borneo, led to the discovery of new and little-known fleas and added considerably to our knowledge of zoogeography. Science is also indebted to these investigators for the encouragement given to other workers to undertake such faunal behavioural and distributional studies.

Additional comments on the genus follow the descriptions of new species below.

1. **Medwayella dryadosa** sp. nov.

Type material. Holotype male (B-45320-1) ex *Rhinosciurus laticaudatus*; MALAYA: Selangor, Gombak Forest Reserve, 16 mi N of Kuala Lumpur; 300 m elev.; Coll. R. Traub for U.S. Army Medical Research Unit (Malaya); 22.VII.1956. Allotype female (B-47809) ex *R. laticaudatus*; MALAYA: Selangor, Ampang Reservoir, Ampang Forest Reserve; 1.V.1958; Coll. R. Traub. The data for 80 ♂ and 51 ♀ paratypes are summarized in Table 1, which cites the hosts and localities represented. Holotype (U.S.N.M. number 71598), allotype and paratypes deposited in the U.S. National Museum, Washington, D.C. Paratypes deposited in the collections of the British Museum (Natural History), Bernice P. Bishop Museum (Honolulu), Field Museum of Natural History (Chicago), the Canadian National Collection (Ottawa), the Division of Medical Zoology, Institute for Medical Research (Kuala Lumpur), the Parasitological Laboratory (Stavropol, Caucasus, USSR), the Rijksmuseum van Natuurlijke Historie (Leiden, The Netherlands), Robert E. Lewis, E. W. Jameson, the author, etc.

Diagnosis. Agrees with *Medwayella robinsoni* in possessing a distinct subapical notch near apex of dorsal (anterior) margin of distal arm of ♂ sternum 9 (figs 20, 21,

TABLE I.

SUMMARY OF DATA FOR COLLECTIONS OF PARATYPES OF *MEDWAYELLA DRYADOSA* SP. NOV. AND *MEDWAYELLA PHANGI PHANGI* SP. NOV. IN MALAYA

Host	Spp. of MED.	1. Kuala Lumpur Forest	2. Subang Forest	3. Ipoh Hills	4. Gunong Benom	5. E. Coast Forest	6. Kelantan Forest	7. Moun-tains	8 Kedah or Perlis
A. *Callosciurus notatus*	M.D.	–	–	–	–		–	–	–
	M.P.	–	1♂ 1♀	–	–	–	–	–	2♂
B. *Sundasciurus tenuis*	M.D.	–	–	–	–		–	–	–
	M.P.	1♂ 1♀	4♂ 11♀	12♂ 7♀	–	–	–	–	–
C. *Tamiops macclellandi*	M.D.	1♂	–	–	–		–	–	–
	M.P.	–	–	–	–	–	–	–	–
D. *Tupaia glis*	M.D.	4♂ 4♀	2♀	–	–	1♂	–	1♂ 3♀	1♂ 1♀
	M.P.	1♂	4♂ 5♀	6♂ 1♀	–	–	–	–	13♂ 5♀
E. *Tupaia minor*	M.D.	–	–	–	–	–	–	–	–
	M.P.	–	1♂	–	–	–	–	–	–
F. *Rattus bowersi*	M.D.	–	–	–	–	–	–	1♂	–
	M.P.	–		–	–	–	–	–	–
G. *Rattus rajah*	M.D.	3♂ 1♀	–		–	–	–	1♀	–
	M.P.	–			–	–	–	–	–
H. *Rattus muelleri*	M.D.	1♂ 1♀	–	–	–	–	–	–	–
	M.P.	–	–	–	–	–	–	–	–
I. *Rattus tiomanicus jalorensis*	M.D.	–	–	–	–		–	–	–
	M.P.	1♂	–	–	–	–	–	–	–
J. *Dremomys rufigenis*	M.D.	–	–	–	–	–	–	2♂	–
	M.P.	–	–	–	–	–	–	–	–
K. *Lariscus insignis*	M.D.	4♂ 3♀	–	5♂ 6♀	–	–	1♂	1♀	–
	M.P.	–	–	4♂ 3♀	–	–	–	–	–
L. *Rhinosciurus laticaudatus*	M.D.	41♂ 21♀	6♂ 4♀	2♂	4♂ 4♀	–	–	–	2♂
	M.P.	4♀	–	–	–	–	–	–	–
M. *Ptilocercus lowi*	M.D.	–	–	–	–	–	–	1♂	–
	M.P.	–	1♂	–	–	–	–	–	–
Totals	M.D.	54♂ 30♀	6♂ 6♀	7♂ 6♀	4♂ 4♀	1♂	1♂	5♂ 5♀	3♂ 1♀
	M.P.	3♂ 5♀	11♂ 17♀	22♂ 11♀	–	–	–	–	15♂ 5♀
Collectors		U.S.A.-M.R.U. I.M.R.	U.S.A.-M.R.U. I.M.R.	U.S.A.-M.R.U. I.M.R.	Lord Medway	U.S.A.-M.R.U.	I.M.R. U.S.A.-M.R.U.	U.S.A.-M.R.U.	U. MALAYA I.M.R.

M.D. = *M. dryadosa* M.P. = *M. p. phangi*

NCH.) and thereby separable from other previously described species in which this arm bears a broad sinus instead of a notch, viz., *M. javana* (fig. 134, ARC.) or else lacks a sinus or notch and instead is merely flattened subapically, viz., *M. loncha* (fig. 127) and *M. rhaeba*. Near *M. robinsoni* but separable as follows: (1) Re distal arm of sternum 9 (fig. 20, *M. dryadosa*; fig. 21, *M. robinsoni*; and cf. fig. 1 for abbreviations of reference points). (a) Apical lobe (fig. 20, AP.L.) (oo–qq) above subapical notch (NCH.) squared or truncate across entire breadth in new species, instead of AP.L. being somewhat rounded dorsally (pp–qq) and usually slightly concave ventrally as in fig. 21 (oo–pp) (AP.L.), or angled (fig. 54). In *M. robinsoni*, even if oo–pp is straight and subvertical, pp–qq is convex (fig. 55). (b) Notch (NCH.) symmetrical, shaped like a rounded "U", instead of lower margin (mm–rr) being more oblique and hence with axis of notch (nn–rr) facing more ventrad, and with lower margin (mm–rr) usually distinctly longer than upper (oo–rr). (c) Transverse sclerotization (T.S.) with lower margin quite straight; not sinuate as in fig. 48 (*M. robinsoni*). (2) Re aedeagus (figs 22, 42, *M. dryadosa*; figs 23, 44, *M. robinsoni*). (a) Thumb-like distal region (THM.) of alpha-portion (ALPH.) of Ford's sclerite (F.SC.) with anterior margin ovate and apex subtruncate; about thrice as long (tall) as broad; whereas in *M. robinsoni* "thumb" (THM.) is more rounded and apex ovate; distal margin about 1·2 times as long as thumb is tall. (b) Lower arm (L.A.) of securifer acuminate subapically, not broad to near apex. (c) Ventral region of phylax (PHY.) scarcely broader than at level near S.I.T. instead of being very much broader. (d) Apex of S.I.T. with ventral margin strongly upcurved and extending well distad of dorsal margin instead of only slightly so. (3) Re ♂ sternum 8. (a) Sternum proportionately taller, viz., only 1·4 times as long (fig. 29, p3–t3) as high (i3–r3) instead of 1·7 times as in *M. robinsoni* (fig. 28). (b) Distance between longest bristle on caudal margin and ventral margin (m3–t3) proportionately greater in *M. dryadosa*, i.e., length of sternum at level of that bristle (l3–m3) only 2·2 times distance m3–t3, whereas in *M. robinsoni* it is 2·7 times. (c) Lumacaudate process (figs 20, 29) (LUM.) relatively shorter and broader and apex less ovate, viz., length (q3–s3) along ventral margin only 1·6–1·8 times height at middle (level n3–o3), instead of 2·8 times. (4) Re sternum 7 of ♀ (7 S.; figs 26, 27, *M. dryadosa*; fig. 49, *M. robinsoni*). (a) Sinus on caudal margin with upper margin sloping at angle of 50° in new species, instead of usually about 30°; an imaginary line connecting lobes of this sinus therefore more than thrice height of ventromarginal lobe below sinus, instead of being subequal. (b) Dorsal margin of sinus sinuate; resulting lower sinus much taller than, but not nearly as long as ventral lobe. This margin evenly convex above sinus in *M. robinsoni*. (c) Dorsal margin of sinus does not parallel ventral margin at all but immediately arches dorsad in new species. In *M. robinsoni* the sinus is really a notch. (d) Dorsal third or fourth of this segment broader than in *M. robinsoni* in that caudal margin here sloping at angle of less than 60° instead of nearly perpendicular. (5) Spermatheca lacking dorsal peak on caudal bulge of bulga (figs 15, 31, B.); in *M. robinsoni*, peak (figs 32, 49, PK.) visible if organ is in proper perspective. (6) Perula of bursa copulatrix (figs 27, 31, P.B.C.) about twice as high as broad instead of three or more times (figs 32, 59, P.B.C.). (7) Mesal tanned genitalic area (figs 26, 31, M.R.8) with ovoid sclerotization near middle of vertical ridge, instead of near upper limit of vertical ridge (fig. 32). (8) Lacking characteristic pair of tanned chords (representing ventral portion of paragenital morion) found just caudad of apex of glandula vaginalis (G.VG.) in *M. robinsoni* (fig. 32). (9) Lacking sclerotized bead-like thickening(s) representing accessory glands in dorsal wall of apical portion of vagina of *M. robinsoni.*

Description. *Head.* (figs 4, ♂; 6, ♀). Anterior margin evenly curved from vertex to ventral margin, arc making a broad semi-ellipse. Front portion of head of ♂, measured horizontally from level of eye-bristle (E.B.) and labral angle (d4–e4 in fig. 2), and vertically from vertex at falx (v3–w3) to ventral margin (f4–g4) of head, about twice as high as long and thrice as long at level of uppermost bristle of row I (z3–a4); in ♀ the corresponding figures are: twice; 2·4 times. With medium and large preantennal bristles arrangeable in 4 rows (the last 3 arbitrary) as shown in fig. 2 (♂). In ♂ first 2 (I and II) subvertical, of 6 and 4 6 bristles respectively; last 2 (III and IV) almost horizontal. Row III, commencing with eye-bristle (E.B.), and Row IV (genal row, G.R.B.) with 3 bristles. With 1 median "supernumerary" bristle (SY.) between rows II and III. ♀ similar but first (uppermost) and fifth bristles of I small; II with 3–4 bristles and "supernumerary" lacking. Eye well developed, reniform, ventrally excised slightly near middle; about 1·4 times as long as high at ventral third; length of eye subequal to that of third segment of maxillary palpus (M.P.). Genal process unspecialized. Maxillary lobe nearly reaching to apex of second segment of labial palpus (L.P.) and to near middle of ultimate segment of M.P. Labial palpus with apical segment nearly 1·5 times length of fourth (penultimate) and extending to near apex of procoxa. Antennal segment 2 with apical bristles scarcely reaching apex of third joint of club. Postantennal region with 3 rows of bristles arranged 5–5(6) 6 in ♂; in ♀: 5 to 7—5 to 7—5 (6) but with a large gap between bristle near lower corner of occiput and second bristle in row, especially in ♀ where space equals length of remainder of row; with an additional long bristle out of line, near antennal groove, below lower placoid.

Thorax. Pronotum dorsally slightly longer than adjacent spines of comb (in ♀ about 20% longer); with 2 rows of bristles, but first row quite short, generally not reaching middle. Pronotal spines about 20 in number (total); base of comb not reaching to vinculum (VC.2); axis of comb very slightly convex, height of arch at lower fourth; lower $\frac{2}{3}$ of spines shallowly concave dorsally and ventral margins paralleling dorsal for proximal half and then narrowing gradually, apices pointed, but at about angle of 45° and thus spines fairly broad to near tip; fourth spine (from bottom) the broadest; about 5·3 times as long as broad at middle; most spines with longitudinal axis somewhat oblique from horizontal, i.e., 4 middle spines, slope about 45° near base. Mesonotum (fig. 9, MSN.) with 6 rows of bristles, including the anteromarginal and submarginal short rows of very small bristles; the rows covering entire length of notum (but flange bare); last row consisting of very long bristles (with tiny intercalaries) and this curving ventrally so that lowest bristle appears in line with penultimate row; last 2 rows terminating near level of overlapping dorsum of mesepisternum (MPS.); second and third rows shorter, and of smaller bristles; with 1 pseudoseta per side and that subdorsal. Mesepisternum (MPS.) with 1 long bristle near ventrocaudal angle and this preceded by an arc of 3 small bristles; with lobe at cephaloventral corner sinuate. Mesepimere (MPM.) with bristles arranged 2–3–1; last contiguous with spiracular fossa. Metanotum (MTN.) with $3\frac{1}{2}$ rows of bristles, of which the first is the half row represented by 2 or 3 members; second extending just below lucodisc. Third vinculum (VC.3) with dorsal surface quite flat except for apical upcurve to point of articulation; axis almost horizontal. Lateral metanotal area (L.M. and fig. 5) with external measurements longer than high at maxima; with internal measurements somewhat so; with 1 long bristle, flanked by 2 small ones, near dorsocaudal angle. Metepisternum (MTS.) with 1 long bristle in upper rear quadrant, in line with long, narrow squamulum (SQ.), which is thrice as long as broad at middle and is inclined ventrocaudad about 20° from horizontal. Metepimere (MTM.) usually with bristles arranged 4–3–3 in ♂, 4–4–3 in ♀, excluding small intercalaries in last row, 1 of which extends above and below row, and which may be double above ventralmost long bristle; with caudal margin evenly biconvex below level of spiracular fossa, the upper lobe 1·5 times height of lower bulge. Spiracular fossa sagittate but with base broad. Ventral margin quite straight and horizontal, dorsal margin sloping from middle to apex so that both margins parallel for basal half; about 1·8 times as long as broad at maximum level.

Legs. Metacoxa (COX. 3) with lateral bristles on apical $\frac{3}{5}$ and these submarginal or nearly so; with a group of 8 thin mesal bristles in 2 rows of 4 on ventral fifth, plus a few small, adjacent but proximal, mesal submarginals. With about 9 small, thin lateral non-marginal bristles scattered over profemur (FM.1) in 2 irregular rows along long axis. Meso- and metafemora with a group of small, widely spaced dorsal submarginal bristles along apical third and 3–4 ventromarginal ones along apical fifth, of which distal 2 quite long; with 2 bristles adjacent to spiniform member of apical pair of stout bristles. Protibia and mesotibia with apical group of stout bristles paired; stout dorsomarginals paired except for fourth pair (from apex). Metatibia (fig. 19) similar but dorsomarginal notches much more pronounced and with 1 stout bristle contiguous to apical group (A.G.) of 2. Fringe of bristles on dorsal (caudal) margin of first protarsal segment extending slightly beyond middle of II. Apical caudal bristle of mesotarsus I and II reaching to middle of II and III respectively; that of metatarsus II nearly reaching middle of III.

Measurements (in micra) of tibiae and tarsal segments (petiolate base excluded) for holotype:

		Tarsal Segments				
Leg	Tibia	I	II	III	IV	V
Pro-	223	84	84	66	42	101
Meso-	336	166	105	72	46	113
Meta-	483	407	253	138	76	125

Tarsal segment V with first pair of stout lateral plantar bristles slightly displaced towards midline on protarsus (fig. 7) and mesotarsus; not on metatarsus (fig. 8). Third pair of plantars not nearly as displaced medially on metatarsus V as on protarsus. With 2 pairs of thin mesal bristles near first lateral plantars on metatarsus V and 1 such pair by second and fifth lateral plantars; with a stouter, median apical pair; 2 such pairs subapical (of these, 1 median); pair of pre-apical plantar bristles near midline; pre-apical plantar hairs well developed.

Abdomen. Tergum 1 (fig. 9, 1 T.) shorter than preceding notum with its flange; with 3 rows of bristles, preceded by 1–3 subdorsals. Basal sternum of ♀ with a patch of about 14–16 small lateral bristles commencing near vinculum (VC.4) and extending in 2 irregular subvertical rows to near lower third of sternum. Terga 2–5 in ♂ and 2–4 in ♀ with 1 subdorsal apical spinelet per side. Unmodified terga in ♂ with first row not reaching level of spiracular fossa and with ventralmost bristle of second row just below fossa. Caudalmost 2 rows in ♀ similar (i.e., fig. 30, 6 T.); first row ¾ length of second and preceded by a rudimentary row of 2–4 small bristles. Abdominal spiracular fossae (fig. 11, 7 SPC., ♂; fig. 26, ibid., ♀) sagittate but narrow, ranging from 2·7 times as long as broad, on tergum 6, to 1·7 times, on 2 T.; at times dorsally sinuate. Typical sterna in ♂ (fig. 11, 7 S., 7 T.) with a subventral row of 3–4 bristles of which ventral 2 long and submarginal; these preceded by 6–8 small ventromarginals in 2 irregular rows. In ♀ (figs 26, 30, 6 S.), these sterna with 3–4 bristles in first row, 5–7 in second and 5-6 in last; at least 4 ventralmost in last row long, as often is ventromarginal of second row. Upper antepygidial bristle in ♂ (fig. 11, A.B.) slightly more than half length of lower; slightly shorter in ♀ (fig. 26, A.B.). 7 T. of ♀ with modified bristles, resembling A.B., as follows: upper one (U.M.B.) submarginal; not quite as dark, nor as stout nor as long as upper A.B. Dorsalmost of lower modified bristles (L.M.B.) virtually contiguous with plate of A.B. and longer than and as stout as upper A.B. and superficially appearing as an antepygidial bristle; ventral one (L.M.B.-2) similar, but ventrocaudad of L.M.B., separated by a distance equal to height of plate of A.B. Lobe above antepygidial bases (U.L. 7) shorter than antepygidial plate in ♂; subequal in ♀. Lower lobe of ♀ 7 T. (L.L. 7) about twice length of A.B. plate; fairly acutely pointed, but margin turning sharply ventrad at level of L.M.B.-2.

Modified Abdominal Segments—Male. Tergum 8 (fig. 11, 8 T.) slightly more than twice as high (along anterior margin) as long at level of base of spiracular fossa; caudal margin extending ventrad only as far as level of subanal sclerite; i.e., scarcely below spiracular fossa; anterior margin terminating at level of ventralmost bristle of 7 T.; with 2–5 small subdorsal bristles near fossa. Spiracular fossa 8 (8 SPC.) right-angled; its ventral arm more than 5 times as long (high) (including region below horizontal or oblique portion) as broad at middle; horizontal section twice as long as broad, and twice as long as middle of upright arm is broad, gradually and slightly broadening from apex (ventral) to base; ventral extension with height equivalent to somewhat less than half diameter of horizontal section. Sternum 8 (8 S. and fig. 29) very large; about 1·3 times as long (p3–t3) as broad (high) (q3–i3) at maxima; extending dorsad above ventral margin of 8 T. and, ventrally, further cephalad than line of antepygidial plate; somewhat trapezoidal, but apparent dorsal margin (h3–j3) convex; and then remainder of true dorsal margin sloping ventrocaudad at angle of 45° to dorsocaudal corner at m3; ventral margin slightly concave at caudal third (q3–s3) or half (and thereafter microdenticulate); caudal margin (m3–t3) shallowly convex or almost straight: anterior margin (p3–l3) curving dorsocaudad at about angle of 60° and then (l3-h3) mainly at 45°. Lumacaudate process (LUM. and fig.

12) arising at middle portion of ventral margin; with truly spinose area nearly twice as long (ventrally, q3–s3) as high (level of o3) at middle; apically subovate or broadly rounded; length of apical lateral seam or fold (S. LUM.) equal to $\frac{1}{4}$ of spinose area; ventral spiniforms in general the stoutest; rest of apical and subapical heavier than median and anterodorsals; the bristles usually in 7–8 rows and about 34–42 in number. 8 S. with a curving suture (SU.8) delimiting a more heavily sclerotized mesal portion; the suture arising near dorsal margin of LUM.; curving dorsocephalad and, at dorsal third, recurving towards summit of dorsal convexity of sternum so that less tanned area commences at base of LUM. and narrows gradually. Considering only bristles caudad of suture and above and behind LUM.: 8 S. with about 18–20 bristles in 4 rows of approximately 5–6–5–4 bristles, those of the last row longer than most, and these well separated between dorsalmost (m3), which is longest, subdorsal and caudomarginal, and a submarginal group of 3 at lower third and fourth; uppermost of third row at caudodorsal corner, near m3; uppermost of second row slightly more dorsal than that of third and anterior by a distance of about $\frac{1}{2}$ its length. Remaining bristles as follows: 1 on LUM. median; a close-set group of 3–4 ventromarginals at base of LUM.; 3 oblique, irregular rows, sloping ventrocaudad, of 5–5–3, which first is anteriormost; these rows preceded by about 4 subventral small bristles. Nude area on 8 S. comprising anteroventral fourth and anterodorsal fifth. Immovable process (figs 11, 14, P.) with dorsal margin fairly straight or shallowly concave near dorsal bristle; with apical bristle more than twice length of dorsal; with caudal (ventral) margin quite straight to marked sinus at boundary with manubrium (MB.). Conical process (C.P.) of P. about 5 times as long (cf. fig. 1, e–h) as broad at middle (f–g); caudal margin fairly straight. Movable finger (F.) with portion distad of P. (s–n) slightly more than twice as long (s–n) as broad at maximum breadth near apex of P. (i–q) and nearly 4 times as long as broad at middle of subapical constriction (j–k); with broadest portion (i–q) about twice breadth of narrowest (j–k). F. with anterior margin quite convex at level of C.P. but soon straightening and then becoming mildly sinuate subapically for arc at bases of sensilla-group (S.G.); posterior margin markedly convex at apex of P. (r–q) but sigmoid so that concavity of upper half equals bulge of lower, with maximum depth of trough (k) at apical fourth. Stiva (STV.) short, the distocaudal expansion (measured from k–o, which denotes a projection of caudal margin if there were no stiva, to point p) slightly less than $\frac{2}{3}$ of j–k and about $\frac{1}{3}$ length of apex of F. (l–p). F. with a sensilla-group (S.G.) stouter but subequal in length to bristles along middle of apical margin. Distal fringe (D.FR.) with lowermost of 4 bristles thinner than its mates; with bases of lower 3 bristles recessed so that they appear somewhat submarginal and, in lower 2 bristles, distance to level where transversed by caudal margin slightly exceeding diameter of bristles at that point. With a widely-spaced group of 3 fairly long, thin bristles near beginning of sinus of caudal margin; with an oblique submedian row of scattered, thin, lateral bristles starting near pair of anterior group of mesal marginals (AN.GP.) above apex of C.P., and continuing distad to level of S.G.; middle portion of these accompanied by a few smaller mesal bristles. Fulcral sclerite (F.S.) shaped like an axe-head with a broad edge; latter (dorsal) (xx–ww) more than twice breadth of apex (zz–a3). Manubrium (MB.) broad, only slightly narrowed from middle to near apex; nearly

twice as long (y to level of a/b) (from ventral margin of tergal apodeme of segment 9, T.AP. 9, to apex) as broad at anterior ventral bulge (at w); apex (y) broad and only slightly upturned; dorsal margin slightly convex; ventral margin somewhat biconvex near base, proximal bulge (w) near level of F.S. T.AP.9 2·5–3 times as long (a/c–b/d) as broad near apex (a–c); longitudinal axis apically somewhat curving towards 8 SPC.; somewhat narrowed at middle. Sternum 9 with proximal arm (P.A.9) with margins diverging from base (gg) at trough of "U." Anterior (ventral) margin (hh–aa) quite straight and oblique (dorsocephalad) to above basal third (dd), and then curving fairly dorsad (dd–aa); upper half shallowly biconcave but with dorsal (anterior) sinus (aa–cc) longer than lower (cc–dd). P.A.9 with caudal (dorsal) margin curving dorsocaudad from trough of "U" (gg) but quite flat or mildly sinuate and in essence almost paralleling dd–aa so that upper ⅔ of P.A.9 (bounded by aa, bb, ff, dd) broadly rhomboidal; and with long axis of rhombus 1·6 × cc–ee, and dimensions of arc aa–bb somewhat exceeding those of dd–ff. Distance aa–cc equals cc–ee. Distal arm of sternum 9 (figs 18, 20, D.A. 9) about 6·8 times as long (ii–qq) as broad at level (uu–jj) of transverse sclerotization (T.S.), which is narrow, straight, except for slight convexity on upper (dorsal) half of anterior (proximal) margin. Subapical notch (NCH.) on anterior (dorsal) margin parallel-sided, its depth (nn–rr) subequal to its height (mm–oo). Apical lobe (AP.L.) somewhat higher (oo–qq) than long (pp to level of rr). Thickening (THK.) at base of supramedial flap (SUP.FL.) well represented along trough of notch and slightly above and below it. Subapical lobe (SUB.L.) below notch extending slightly more dorsad than AP.L. (mm higher than pp); with a small group of thin submarginal bristles below SUB.L. Subapical group of short spiniforms (S.G.SPN.) 4 to 5 in number, with distalmost the smallest and at level of base of NCH. and basalmost at level of SUB.L. Subapical patch of "sensory" microspicules (MSP.P.) extending from near upper margin of NCH. to supramedial group (SUP.G.) of 5 thin bristles. Caudomarginal submedian group (CM.G.B.) consisting of 3 stout bristles, of which bases of upper 2 frequently overlap; with 2 much smaller, thinner marginal bristles distad of these. Mid-microspiculate area (M.MSP.) elongate-ovate, equivalent to ⅙ length of D.A.9 and its cavity extending into arm for about ⅓ depth of latter, its apex on anterior (dorsal margin) (kk) well separated from proximalmost bristle of group below SUB.L., at point ll.

Aedeagus—Lateral Aspect. Aedeagal apodeme (fig. 10, AE.A.) with middle lamina (M.LAM. and fig. 22) more tanned than lateral laminae (L.LAM.). Middle lamina about 4 times as long (from anterior edge of crescent sclerite, figs 23, 93 (C.S.) at base of aedeagal fulcrum, AE.F. to apex) as broad at anterior margin of bay of middle lamina (B.M.L.); anterior ⅔ gradually narrowing. Apex of apodeme upturned, and plates fusing to a point just below tip, which is nearly thrice as long as broad. Apodeme somewhat constricted at level of caudal portion of caverna spiculosa (CAV.SPIC.), basad of AE.F. Lateral laminae with ventral and anterior margins primarily paralleling that of M.LAM. Bay of middle lamina (B.M.L.) extending cephalad ⅗ of length of apodeme (from AE.F.). Median dorsal lobe (M.D.L.) (and fig. 42) straight but oblique at angle of about 15° commencing at constriction of AE.A. to level of middle of sclerotized inner tube (S.I.T.); here becoming markedly rounded but curving ventrad only as far as line of basal portion, at origin of hood

(HD.). Aedeagal pouch with girdle (G.) well sclerotized but narrow; ventral walls (AE.P.–V.) more tanned than girdle and lateral portions (AE.P.–L.) continuing to level of base of S.I.T.; ventrocaudal region marked by a sclerotized ovate area extending to near middle of lower margin. Hood (HD.) with a deep sinus on lower half of caudal margin; sinus reaching to near apex of sclerotized inner tube (S.I.T.) and its depth somewhat less than that of resulting lobe beneath it; this ventral lobe subtruncate dorsally and evenly and strongly convex below as margin of hood continues anterodorsad as triangular deltoid flap (DEL.FL.). Margins of DEL.FL. forming angle of 45° at junction above level of AE.F. and apex somewhat extended, acute; dorsal edge of flap blending caudally with upper apex of body of crochet (B.CR.) at base of alpha-portion (ALPH.) of Ford's sclerite (F.SC.). Ventral margin of DEL.FL. an arc whose trough is in line with bottom of phylax (PHY.) and covers region of "crochet." Lateral lobes (L.L.) extending caudad from ventral margin of AE.P. as a shallow sinuate structure and then arching to blend with lateral walls of aedeagal pouch (AE.P.–L.) and with crochet-process (CR.P.) to form quasi-crochet (Q.C.), all of which are mesal to overlapping deltoid flap (DEL.FL.). Ford's sclerite (F.SC.) largest of structures in endchamber; its alpha-portion (ALPH.) basally rectangular; its anterodorsal margin fairly straight to curve of thumblike distal section (THM.), which is short, apically truncate; curved axis of thumb about twice as long as tube-like arch is broad. Securifer (SEC.) of F.SC. chelate (in appearance) apically; dorsally biconvex, i.e., base of upper arm (U.A.) commencing as ovate structure arising near thumb of ALPH., becoming concave at caudal fourth and then with free portion of U.A. extending apicad as a narrow arched rod which is almost claw-like or falcate; with proximal axis of free section nearly horizontal and essentially an extension of that of main body of upper arm, i.e., not angling dorsally. Lower arm (L.A.) of securifer sinuate dorsally and acuminate at apex as the opposite member of the "chela." Pivotal ridge (PIV.R.) relatively lightly sclerotized; rod-like to apex at summit of phylax (PHY.) and base of F.SC. With pivotal chord (PIV.CD.) fairly straight close to basal wall of ALPH. and terminating at a root-like extension from base of U.A. Sclerotized inner tube (S.I.T. and fig. 43) lacking distinctive armature; about 9 times as long as broad at straight portion of middle; very broad basally but rapidly narrowing to a constriction at level of anterior margin of PHY., where it bulges dorsally and ventrally (with curved margins); length of dilated portion shorter than diameter; tube only slightly convex to a short dorsal spur at distal fourth and then becoming somewhat upcurved to apex; with a membranous connection between the spur and apex of tube; ventral margin extending distad of apex as a short, sinuate rod-like projection; distal fourth bearing sclerotized ring-like ridges. Crescent sclerite (C.S.) shallowly convex; about 2·5 times as long as S.I.T. is broad at middle. Satellite sclerite (SAT.S.) very small, scarcely exceeding depth of C.S. Fulcral lateral lobes (FUL.L.L.) narrow; relatively lightly tanned. Central sclerite (CEN.S.) closely approximating fulcral medial lobe (FUL.M.L.). Y-sclerite (Y.S.) conspicuous as a diamond-shaped structure below fulcrum and with a narrow branch (in lateral aspect) extending distad as floor of capsule. Dorsal virga (D.V.) lightly tanned. Lateral shafts of capsule (L.S.C.) well sclerotized from level of C.S. to ventral margin of FUL.L.L., their tendons (T.L.S.) lightly tanned. Phylax

(PHY.) conspicuous; its altitude (vertical length) about twice breadth of base; proximal half only slightly narrowing; curving dorsocaudad at upper level of S.I.T. Body (basal sclerite) of crochet (B.CR.) as long as crochet process (CR.P.); length of expanded apex equivalent to half of height of B.CR., apparently constituting major or entire component of dorsal, longitudinal portion of quasi-crochet (Q.C.); this tanned element directed caudad as an arm subequal in girth to that of B.CR.; about 6 times as long as broad at middle; slightly broadened subapically; apex broadly pointed; dorsal margin almost straight and ventral margin corresponding. Spiculose lobe (SPIC.L.) (apparent homologue of median lamella) extending below Q.C. for distance equal to half breadth of latter. Vesicle (V.) fairly well developed. Penis rods (P.R.) not extending beyond up-curve of AE.A. Apodemal rod of endophallus (third aedeagal rod) (A.P.R.) fairly well tanned to apex, near that of P.R. Ventral virga (V.V.) well developed and tanned far beyond (cephalad) level of girdle (G.).

Aedeagus—Dorsal and Ventral Aspects. (fig. 24, dorsal; fig. 25, ventral). Ford's sclerite (F.SC.) basally fused along midline. Apical half (U.A.) bifid, the cleavage extending far proximad for L.A. and ALPH. Apical lobes of U.A. broadly pointed; rather spatulate; acuminate in L.A. Aedeagal pouch not completely enclosed ventrally, its thickened ventral walls (AE.P.–V.) V-shaped, with divergence terminating at base of phylax (PHY.) and origin of lateral lobes (L.L.), which distally blend with lateral margins of aedeagal pouch (AE.P.-L.). Wall of aedeagal pouch merging with sides of crochet process (CR.P.) to form quasi-crochet of lateral aspects. Phylax (PHY.) sloping towards midline from base to apex. Spiculose lobe (SPIC.L.) arising at base of phylax and extending caudad to near apex of CR.P. Deltoid flap (DEL. FL.) triangular at caudal end as well as cephalic; covering lateral thirds of dorsal surface from origin at apex of basal sclerites of crochets (B.CR.) to level of fulcrum; likewise ensheathing sides of ventral portion of endchamber as a development of hood (HD.). Ring-like transverse sclerotizations on apical portion of S.I.T. not completely encircling tube, i.e., are ridged arcs. Crescent sclerite (C.S.) narrowed caudally as it approaches midline. Satellite sclerite (SAT.S.) along dorsal midline, immediately distal to apices of crescent sclerites and directed into chamber of sclerotized inner tube (S.I.T.). Lateral shafts of capsule (L.S.C.) appearing as long, triangular structures between lateral lobes of fulcrum (FUL.L.L.) and fulcral median lobes (FUL.M.L.) and extending to near apex of C.S. Tendons of lateral shafts (T.L.S.) arising from their bases and continuing far cephalad. Y-sclerite (Y.S.) serving as floor for capsule, with one fork or fold terminating near apex of C.S.; the other broader, butterfly-shaped, and the length of FUL.L.L. Central sclerite (CEN.S.) a bell-shaped structure superimposed upon FUL.M.L. Ventral virga (V.V.) bifid at apex. Caverna spiculosa (CAV.SPIC.) elongate, subdorsal ovate sinuses, extending from near base of bay of middle lamina cephalad towards base of aedeagal pouch.

Female. (figs 26, 27, 30). Sternum 7 (7 S.) about 1·6 times as high as long at maximum diameters; anterior margin nearly vertical save for dorsal slope towards short dorsal margin; caudal margin with upper half shallowly sinuate and lower half with a large sinus whose lower margin slopes ventrocaudad at a 45° angle and upper margin is slightly biconcave (the component arcs subequal in shape and size) and slopes dorsocaudad at 40°; upper lobe of sinus broadly rounded; lower lobe truncate and about twice as long as broad at middle. Sternum 7 with 3 rows of bristles following a group of 2–4 small ventromarginals; first irregular and with about 10 small bristles, second with about 9, slightly longer and of these, 2 ventromarginal; third with 6 long bristles of which 1 is submedian, at level of anal stylet (A.S.), 2 near middle of upper lobe of sinus and 3 at base of lower sinus, including 1 ventromarginal and 1 sub-ventromarginal; of latter 3 on ventral lobe, anteriormost much closer to ventral member of preceding pair than to dorsal one. Tergum 8 (8 T.) with caudal margin shallowly concave to level of A.S., then quite straight and oblique to a fairly narrow lobe at ventrocaudal angle; this lobe about twice as long as broad at middle. 8 T. with an irregular row of 5 short bristles immediately in front of spiracular fossa (8 SPC.) and this preceded by 1–2 similar bristles, at times by a more anterior, smaller, dorsomarginal; vental pair of mesal marginal genitalic bristles immediately above ventrocaudal lobe twice as long as those at base of ventral anal lobe (V.A.L.); with an oblique, horizontal row of 5 bristles near ventral margin, commencing near middle of margin and terminating at level of upper base of lobe at anteroventral angle, but anterior to it; last 3 of this row the longest; with another 2 similar rows slightly dorsad to sub-ventromarginal one, but these bristles smaller, although terminal ones get progressively longer; with a fourth such row represented merely by 1–3 bristles dorsal to these. Mesal genitalic ridge of 8 T. (M.R.8) with anterior, vertical margin slightly sinuate or almost straight; with a crescentic (quarter moon) sclerotization buttressing this, commencing at midline and continuing to subdorsal region; below the crescent, an indiscrete or Y-shaped tanned area. Dorsal anal lobe (D.A.L. and fig. 16) with anterior dorsal half and ventral two-thirds nude; remainder of surface clothed with 2 or 3 rows of bristles, of which only last complete and consisting of long bristles, especially the one above, and, particularly that below, base of anal stylet (A.S.); with an additional very long bristle at dorsocaudal angle. Anal stylet broadest near base; quite straight and cylindrical thereafter, but at times slightly narrowed at apical fourth (especially ventrally); about 4 times as long as broad at middle; with a very short dorsal bristle at base of long apical bristles; at times with a tiny ventral 1 there as well. Ventral anal lobe (V.A.L.) with distal margin bearing a pair of bristles at basal angle, viz., 1 large and 1 small; a pair of long ones near basal fifth; a very long one beyond midpoint and an adjacent smaller one (at apical $\frac{2}{3}$) and, at times, a virtually contiguous small one further distad.

Spermatheca (SP. and figs 15, 27, 31) shaped like a peanut in which the caudal lobe is foreshortened[3] and broader than the other, i.e., bulga (B.) dorsally somewhat constricted at basal third; proximal portion somewhat more convex than anterior (but lacking a distinct dorsal peak) and caudal margin somewhat flattened. Bulga about twice as long (from anteroventral angle) as broad at narrowed area; ventral margin a long, shallow arc. Hilla (H.) with nearly half its length internal; slightly more than 4 times as long (total length but excluding apical papilla, PAP.) as broad at point of entry (ignoring thickenings of wall). Apical papilla well developed, longer than high. Duct of spermatheca (D.SP. and figs 27, 31) with section entering bursa copulatrix dilated (DIL.P.) as compared to remaining ¾ of length; sclerotized internal rings best developed in region anterior to dilated section. Bursa copulatrix (B.C.) with perula (P.B.C.) ovate-oblate; anterior margin straight and vertical; caudal margin somewhat convex; twice as high as broad. Sac of bursa copulatrix (SAC.) semimembranous and dilating at level of middle of perula and extending above it for distance of 1·5–2 times breadth of P.B.C. Duct of bursa copulatrix (D.B.C.) below perula biconcave, with the arch usually quite pronounced. Duplicatura vaginalis (D.VG.) marked by an oblique sclerotization and entering at undifferentiated lura of bursa copulatrix. Glandula vaginalis (G.VG.) appearing a short, oblique slit at the termination of the virtually horizontal, somewhat thickened and muscled roof of the vagina (VAG.) near genital chamber. With an accessory "gland" (fissure) immediately anterior to G.VG. Paragenital morion (PG.M.) reduced (in mounted specimens), usually represented on each side as a narrow, short, constricted horizontal "U" near P.B.C. and whose dorsal and ventral branches are virtually contiguous and whose open end is caudad, the lumen between branches at times tanned and appearing as a short rod. Occasionally dorsal loop of PG.M. visible as an indiscrete longitudinal, membranous area extending towards ventral portion of sternum 9 (9 S.). Eighth sternum (8 S.) usually with 1 or 2 dorsal short bristles, a longer dorsal subapical one and a terminal one; apically narrow, viz., portion distad of level of most proximal bristle equal to twice breadth (height) of sternum at this level; longest bristle about 4 times this breadth.

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[3] It is too bad that there is no such term as "hind-shortened," for that would be more pertinent and descriptive.

ILLUSTRATIONS

4. Head and prothorax (♂)
5. Lateral metanotal area (♂)
6. Head (♀)
7. Apical segments of protarsus
8. Segment 5 of ♂ metatarsus
9. Meso- and metathorax
10. Aedeagus
11. Modified abdominal segments (♂)
12. Lumacaudate process
13. Dorsal and ventral anal lobes (♂)
14. Processes of clasper
15. Spermatheca
16. Anal lobes and stylet (♀)
18. Clasper and sternum 9
19. Metatibia (♂)
20. Distal arm of sternum 9
22. Apical region of aedeagus (lateral aspect)
24. Apex of aedeagus (dorsal aspect)
25. Apex of aedeagus (ventral aspect)
26. Modified abdominal segments (♀)
27. Spermatheca, genitalia and anal segments
29. Sternum 8 (♂)
30. Segments 7 (♀)
31. Genitalia (♀)
42. Apex of aedeagus
43. Sclerotized inner tube
93. Apical region of aedeagus

COMMENT. It is noteworthy that although the great majority of the long series of *M. dryadosa* were from squirrels, all of the actual hosts were species that spend all or most of the time on the ground, i.e., there were no true tree-squirrels represented. Thus, out of 1421 squirrels (excluding flying-squirrels) and tupaiids examined personally by the writer or the staff of the U.S. Army Medical Research Unit (Malaya), 149 were ground-squirrels of the genera *Lariscus* (52 specimens examined), *Rhinosciurus* (23) and *Dremomys* (74), as shown in Table 2 (p. 259), which summarizes the host-relationships of 3 Malayan *Medwayella*. These rodents nest amongst the roots of trees, etc., rather than high on the branches of the tall trees characteristic of the

Malayan forest. The other hosts occasionally reported were either ground-dwelling rats like *Rattus rajah*-group or *R. muelleri* or, like *Tupaia* (237 examined), were abundant on the ground-surface, although scansorial. In contrast, although 624 truly arboreal squirrels, such as *Callosciurus nigrovittatus* (110), *C. notatus* (259), *C. caniceps* (184), *C. prevosti* (18) and *Sundasciurus hippurus* were carefully checked for fleas, no *M. dryadosa* were ever found on them even though they inhabited the same localities and habitats as the ground-squirrels, and even though they at times carried other species of fleas. Even the 348 specimens of the small species of *Sundasciurus* (*S. tenuis* and *S. lowi*) were found to be uninfested with this new species of *Medwayella*, despite the fact that these squirrels often descend to the forest floor (but nest in trees). It also is significant that *M. robinsoni*, in contrast, could be found on any of these hosts, regardless of where they nested.

The name *dryadosa* reflects the host-relationships of this new species and derives from the Greek words *drys* or *dryas* for tree (or even from *dryados*, meaning tree-inhabitant) and *osor*, or hater. The reason for the "antipathy" of *M. dryadosa* for tree-squirrels is unknown, but it seems likely that two factors are involved, viz.: (1) Conditions in the arboreal nests of these squirrels may not be suitable for the immature stages of the flea. (2) Tree-squirrels do not spend enough time on the ground to acquire significant numbers of "strays" of *M. dryadosa*. Data concerning the 4 other species of *Medwayella* known to occur in Malaya (new species, described below) lend support to this hypothesis. Thus, all of these parasitize ground-squirrels and 2 of them have virtually never been taken on truly arboreal squirrels like *Callosciurus*. It is odd that while the fleas of ground-squirrels rarely, if ever, infest tree-squirrels, a species of flea (*M. robinsoni*) relatively common on the arboreal mammals should be reported from all the ground-dwelling species, and, indeed, at times be as prevalent on these hosts as are their "characteristic" fleas. This point is discussed further below (p. 233).

Among the ground-squirrels, *Rhinosciurus laticaudatus* was the main host for *M. dryadosa*, accounting for 65% of the records even though fewer *Rhinosciurus* were examined than any other species of small mammals listed (except for *C. prevosti*). Further consideration of the host-relationships is deferred until the end of the descriptive portion dealing with *Medwayella* in this paper (p. 258).

M. dryadosa was collected in all the non-coastal forested areas surveyed in Malaya by USAMRU, by the DMZ-IMR and by the University of Malaya, provided ground-squirrels were examined in sufficient numbers. The records include areas as far north as Kelantan and Gunong Benom. Four specimens (3 from *Lariscus*) were taken on Tioman Island, off the southeast coast of Malaya, suggesting that the species probably ranges to the forests near the east coast (where inadequate collections have been made). Altitudinally, the species is known to range from the lowland dipterocarp forest of Subang (800 ft) and Gunong Benom (700 ft) to montane forest near the summit of Mt. Brinchang at 6600 ft elevation.

2. **Medwayella arcuata** sp. nov.

TYPE MATERIAL. Holotype ♂ ex *Tupaia* sp.; INDONESIA: Sumatra, Suban Ajam, Redjang, Bengkoelen (Benkoelen or Bengkulu); July, 1916; Coll. E. Jacobson (in the mountains 20 km from Benkoelen town, approximately 3° 15′ S, 102° 25′ E, fide F. G. A. M. Smit, in litt.). No other specimen known. Holotype deposited in Rijksmuseum van Natuurlijke Historie (Leiden).

Diagnosis. Separable from all described species except *M. javana* in that dorsal margin of distal arm of sternum 9 (fig. 33) is deeply arcuate subapically and hence lacking the true notch (NCH.) of *M. dryadosa* (fig. 20) and *M. robinsoni* (fig. 21) or flattened apicodorsal margin of *M. loncha* (figs 3, e3–qq; 127) and the new species next described (fig. 68, HOM.) and their allies. Near *M. javana* but separable as follows: (1) Movable finger (fig. 34, F.) much broader throughout, viz., portion distad of apex of immovable process P. about twice as long (cf. fig. 1, r–n)[4] as F. is broad at level of apex of conical process of P. (C.P.) (i–q) instead of about 4 times as in *M. javana* (fig. 133, F.) while length (r–n) is about 4 times breadth at level of middle of subapical constriction (j–k), not 5 times. (2) Due to curve of arc of bases of bristles of distal fringe (D.FR.), distance from uppermost bristle to apex of F. equals approximately $\frac{1}{3}$ of that to most dorsal part of curve at group of sensilla (S.G.) (l), instead of being subequal. (3) Subapical dorsal sinus (fig. 33, ARC.) deeply and almost evenly arcuate, nearly thrice as long (chord between tips of SUB.L. and AP.L., e.g., mm–pp) as deep at trough, not 5 times because of shallow depth (fig. 134, ARC.), nor with apical lobe (AP.L.) extending more dorsad than subapical lobe (SUB.L.). (4) Lower arm of securifer (fig. 98, L.A.) with caudal margin slightly sinuate and subacute at ventrocaudal angle, instead of being oblique and truncate (fig. 95). (5) Tanned portion of quasi-crochet (Q.C.) tantamount to crochet-process (CR.P.), longer and narrower in new species, i.e., nearly 4 times as long as broad at middle, instead of 2·5 times.

Descriptive notes. Otherwise essentially as in *M. dryadosa*, except as follows: Distal arm of sternum 9 with bristles between those of caudomedial group (fig. 33, CM.G.B.) and subapical group of spiniforms (S.G.SPN.) quite stout. Thumb (fig. 98, THM.) of Ford's sclerite resembling *M. robinsoni* in being short and curved. Dorsal margin of upper arm of securifer (U.A.) quite sinuate, the resulting anterior lobe subequal to length and curve of claw-like extension of U.A. Base of phylax with a pronounced caudal bulge.

Illustrations

33. Distal arm of sternum 9
34. Processes of clasper
98. Apical region of aedeagus

Comment. The name of the species is based upon the characteristic shape of the upper, anterior portion of the distal arm of sternum 9 and is the Latin adjective *arcuata* meaning bowed or curved.

3. **Medwayella angustata** sp. nov.

Type material. Holotype ♂ and allotype ♀ ex "*Sciurus nigrovittatus* and *Lariscus niobe*" (= *Callosciurus nigrovittatus* and *L. insignis niobe*); INDONESIA:

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[4] Compare with fig. 1 for abbreviations of reference points used in measurements.

W. Sumatra: Sipora Island; Nov. 1924; Coll. C. Boden Kloss. Paratypes: 1 ♂, ibid.; 1 ♂, 1 ♀, ibid., but ex *C. nigrovittatus* (all from N. C. Rothschild Collection at British Museum (Natural History)). Holotype, allotype and 1 ♂ paratype deposited in collection at Tring. 1 pair of paratypes in collection of R. Traub, with ultimate deposition in the U.S. National Museum.

Diagnosis. Near *M. dryadosa* regarding truncate margin of apical lobe (fig. 36, AP.L.) of distal arm of sternum 9, etc., but separable as follows: (1) Alpha-portion (fig. 45, ALPH.) not terminating in a "thumb" (cf. figs 22, 42, 93, THM.) but, instead, with tanned portion apically rod-like and with a semi-membranous truncate extension joining base of upper arm (U.A.). In *M. dryadosa*, ALPH. terminates in a subquadrate thumb-like process thrice as long (tall) as broad. (2) Securifer with base of upper arm (U.A.) less than 1·5 times length of extended snout-like or digitoid portion, instead of being more than twice its length (measured from edge of internal vertical root. (3) Distal ⅖ of extended portion of lower arm (L.A.) acuminate, fairly straight; instead of with subapical portion narrowed significantly, and this portion up-curved. (4) Phylax (PHY.) relatively broad, i.e., only about 1·6 times as long as broad at base instead of twice as long. (5) Base of PHY. with caudal margin more convex than anterior margin which is quite straight ventrally; instead of vice versa. (6) Tanned portion of quasi-crochet (Q.C.) relatively broader, i.e., length (measured from caudal margin of phylax) only about 4·4 times girth at middle instead of 5 times. (7) Anterior ventral bulge of manubrium (cf. fig. 1, w) much more pronounced than bulge (u) caudad of sinus (v) instead of both being subequal and shallow. (8) Distal arm of sternum 9 (fig. 36, D.A.9) with notch (NCH.) asymmetrical in that lower margin (mm–nn) is longer than upper one (nn–oo), instead of notch being symmetrical, the upper and lower margins subequal (fig. 20). (9) Notch comparatively shallow, its depth (measured along edge of apical lobe, AP.L.) at middle (nn–rr) hardly more than ⅓ breadth of AP.L.; in *M. dryadosa* it is more than ⅔. (10) Upper margin of AP.L. convex before truncate apex instead of being quite flat to squared apex. (11) Female sternum 7 (figs 37, 38, 41, 7 S.) with dorsal margin of subventral sinus paralleling ventral margin for at least basal half instead of diverging almost immediately (figs 26, 30, 31). (12) With a well developed vaginal "gland" caudad to glandula vaginalis (G.VG.). This is lacking in *M. dryadosa*. (13) Paragenital morion weakly tanned, represented only by two pairs of short sclerotized parallel lines; one set at apex of G.VG. and one somewhat more anterior (fig. 41); lacking the longer rod-like sclerotization near perula of *M. dryadosa* (fig. 31, PG.M.).

Also resembling *M. robinsoni* but readily distinguishable as follows: (1) Alpha-portion (fig. 45, ALPH.) not terminating in a "thumb" (cf. fig. 23, THM.) but instead with tanned portion narrowing apically, rod-like. (2) Snout of upper arm (U.A.) relatively long and narrow, fairly straight or slightly bowed, i.e., digitoid, but very gradually narrowing from base to apex; about 5 times as long as broad at middle instead of being only 2·5–3·5 times as long as broad, more rapidly narrowing from base, and distally fairly broad. (3) Tanned dorsal margin of basal ⅗ of U.A. (the non-digitoid portion) of almost uniform breadth throughout, instead of being much broader proximally than distally. (4) Distal arm of sternum 9 (fig. 36, D.A.9) with apical lobe (AP.L.) truncate nearly its entire breadth, with only upper corner rounded instead of with upper $\frac{1}{3}$ or $\frac{1}{2}$ convex (figs 21, 47, cf. also fig. 1, pp–qq) or at least oblique (fig. 54). (5) Notch (NCH.) in D.A.9 relatively shallow; its depth measured from level of inner edge of AP.L. (nn-rr) is only $\frac{1}{3}$ breadth of AP.L., instead of exceeding $\frac{2}{3}$ of its breadth. (6) Male 8 S. with apparent dorsal margin much longer than in *M. robinsoni*, i.e., not curving appreciably ventrocaudad until well beyond apex of immovable process P. instead of curving well proximad of apex of P. (fig. 28). (7) Lumacaudate process (fig. 39) relatively broader, i.e., the portion distad of internal seam (S.LUM.) only about 67–75 % of breadth of LUM., instead of being subequal to it (fig. 28, LUM.). (8) Anterior (ventral margin) of proximal arm of 9 S. with apical sinus (aa–cc) well developed and ventral one (cc–dd) inapparent, while both are visible in *M. robinsoni* (figs 1, 47) but aa–cc is hardly larger than cc–dd. (9) Sinus in ♀ 7 S. fairly symmetrical, i.e., dorsal margin only slightly diverging from degree of curve of ventral margin (figs 37, 41) instead of clearly doing so at apical half or two-thirds (fig. 49). (10) With a relatively tall and distinct "gland" at dorsal wall of vagina caudad of glandula vaginalis (G.VG.) (although smaller in paratype than in figure 41, which is of allotype). In *M. robinsoni* there is a small, bead-like gland here. (11) Mesal genital ridge of ♀ 8 T. (figs 37, 38, 41, M.R. 8) with dorsal, horizontal tanned area convex ventrally, not sinuate (figs 32, 49) and ventral tail-like portion shorter and stouter, about 1·5 times as long as broad, not 3–5 times. (12) Lobe at ventrocaudal angle of 8 T. ovate, not acute.

DESCRIPTIVE NOTES. Essentially like *M. dryadosa* except as indicated above, and as follows. Tergal apodeme of segment 9 with ventral margin evenly convex instead of sinuate. Tergum 7 of ♀ with caudal margin relatively flat, not curving caudad to or beyond level of apex of lobe (L.L.7) below antepygidial bristles. Ventral margin of spiracular fossa 8 of ♀ straight.

ILLUSTRATIONS

35. Processes of clasper
36. Distal arm of sternum 9
37. Modified abdominal segments (♀)
38. Spermatheca, genitalia and anal segments
39. Lumacaudate process
41. Genitalia (♀)
45. Apex of aedeagus

COMMENT. The name *angustata* is derived from the Latin term for *narrow*, and refers to the appearance of the apex of the alpha-portion and of the upper arm of the securifer.

4. **Medwayella robinsoni** (Rothschild, 1905) NEW COMBINATION

Ceratophyllus robinsoni Rothschild, 1905, Novit. zool. 12:483, fig. 6.

Pygiopsylla robinsoni, Rothschild, 1906, Ent. mon. Mag. (2) 17:221; Rothschild, 1908, Proc. zool. Soc. Lond. 50:617; Oudemans, 1909, Notes Leyden Mus. 31:195, fig. 1; Rothschild, 1919, J. Fed. Malay States Mus. 8(3):5, pl. 2, figs 4, 5; Jordan & Rothschild, 1922, Ectoparasites, 1:230, figs 223, 224.

Stivalius robinsoni, Jordan & Rothschild, 1922, Ectoparasites, 1:259, figs 223, 224; Costa Lima & Hathaway, 1946, Pulgas: 324; Traub, 1950, Proc. ent. Soc. Wash. 52(3):121; Traub, 1951, Proc. biol. Soc. Wash. 64:11, pls. 2, 4; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 7(2):41.

DIAGNOSIS. The features cited in the comparison of *M. dryadosa* with *M. robinsoni* serve as a diagnosis, but since *M. robinsoni* is a widespread species, ranging at least as far as Borneo and Indonesia, and subspecies exist, salient characters at the species-level are now cited. (1) Thumb (figs 23, 44, THM.) of alpha-portion (fig. 46, ALPH.) of Ford's sclerite short and in the "cocked" position; apically flattened and with rounded corners; somewhat longer (broader) at apex than stem is tall; anterior margin convex, posterior margin concave. (2) Upper arm (U.A.) of securifer with base quite flat dorsally and slightly exceeding THM. in height; apex digitoid but broader at base and slightly arched. (3) Lower arm (L.A.) almost as high as long at base; caudal margin oblique (75°) and quite straight; with a short, narrow lobe at ventrocaudal angle. (4) Phylax (PHY.) about 1·7 times as high as broad at base and somewhat expanded subventrally. (5) Tanned portion of quasi-crochet (Q.C.) straight; at least thrice as long as broad at middle; apical margin angled subdorsally. (6) Sclerotized inner tube long and narrow; broadest near base and then slightly arched for $\frac{1}{6}$ of length; straight thereafter; with long, oblique dorsal spur. (7) Hood (HD.) with sinus fairly deep, extending to apex of S.I.T. (8) Distal arm of sternum 9 (figs 21, 53–55) with conspicuous notch (NCH.) which is subequal—lower margin (mm–rr in fig. 1, *q.v.*) longer than upper (oo–rr), and usually conspicuously so. (9) Apical lobe (AP.L.) of D.A.9 with margin (qq–oo) sinuate; upper half (qq–pp) convex; lower half (pp–oo) straight or slightly concave. (10) Subapical group of spiniforms (S.G.SPN.) about 4 in number, short and fairly evenly spaced. (11) Transverse sclerotization (fig. 48, T.S.) somewhat sinuate. (12) D.A.9 lacking a ventro-apical rod-like extension (unlike *M. loncha* and allies, figs 3, 111, EXT.9). (13) Proximal arm of sternum 9 (P.A.9 and fig. 63) with upper half (aa–dd) of anterior (ventral) margin shallowly sinuate; upper concavity (aa–cc) taller than lower (cc–dd). (14) Posterior (dorsal) margin of P.A.9 with upright part (ff–bb) quite straight. (15) Movable finger (figs 17, 47, F.) fairly broad; region (n–s) distad of immovable process P. slightly less than 4 times as long as broad (j–k) at subapical constriction and only scarcely more than twice as long (n–s) as broad at maximum dimensions (i–q) near level of apex of conical process (C.P.). (16) Stiva short and bluntly ovate; apex of F. (l–p) about 2·2 times as long as stiva (p–o/k). (17) Sternum 8 (fig. 28) with apparent dorsal margin (h3–j3) relatively flat and very short due to slope of anterior and "posterior" margins (but actually extending to ventral third—to m3), region h3–j3 only about $\frac{1}{4}$ length of ventral margin. (18) 8 S. relatively long, its ventral length (p3–t3) about 1·5 times maximum height (i3–r3). (19) Lumacaudate process (LUM.) fairly long and narrow, nearly thrice as long ventrally (q3–s3) as broad at level of o3. (20) Female sternum 7 (figs 32, 49, 7 S.) with subventral sinus with dorsal margin usually paralleling ventral margin for about $\frac{1}{3}$–$\frac{1}{2}$ length of sinus, notch therefore generally fairly symmetrical basally. (21) Lobe below 7 S. slightly broader than sinus, of same length, and subtruncate. (22) Spermatheca (figs 32, 52) with bulga (B.) about twice as long as broad in somewhat constricted middle; with a short dorsal peak (PK.) on caudal bulge; inner dorsal margin flat on apex of anterior bulge. (23) Hilla (H.) with anterior margin entering into bulga for nearly $\frac{1}{2}$ its length, of uniform diameter except for distinct apical papilla. (24) Perula of bursa copulatrix (P.B.C.) narrowly ovate but for flattened anterior margin. (25) Sclerotized sectors of paragenital morion appearing (per side) as a single long rod above glandula vaginalis (G.VG.) and a pair of short rods near top of G.VG. (26) With an accessory gland accompanying well developed G.VG. and nearly as large; with 2 or 3 characteristic bead-like glands lining upper wall of vagina near genital chamber, viz.: 1 or 2 near G.VG. and, at times, 1 at apical fourth. (27) Mesal genitalic ridge of 8 S. (M.R.8) resembling a "T" on edge, and with lower arm quite long and narrow; darkest at and above cross-bar, which is curved and sinuate. (28) Third vinculum (fig. 50, VC.3) with dorsal surface quite even. (29) Squamulum (SQ.) parallel to long axis of body; about 3·2 times as long as broad at middle.

COMMENT. *M. robinsoni* was described from a single female specimen collected from *Callosciurus nigrovittatus* in southern Thailand at Nawng Chik, in Pattani, one of the regions formerly called a "Siamese Malay State," and at 6° 53′ N, 101° 15′ E (fide F. G. A. M. Smit, in litt.). In 1919 Rothschild described the male "*Pygiopsylla robinsoni*" on the bases of a pair from *Tupaia tana*, from Korinchi, West Sumatra, apparently overlooking the treatment and illustration of the male by Oudemans, 1909, which referred to two pairs from a nest of *Callosciurus notatus* in Batavia. Rothschild also alluded to a pair from Java, also from *C. notatus*. In 1922, Jordan & Rothschild mentioned additional Sumatran records and illustrated variations in the spermatheca. Later in 1922 these authors summed up the records, including Oudeman's, and pointed out the "♂ is easily recognized by the spinulose process which lies on each side beneath the ninth segment." This presumably was considered so diagnostic that no further description was given at the time, nor was the male ever adequately figured by these workers. This is unfortunate, since the Indonesian specimens represent different subspecies from the mainland *robinsoni*, as is shown below. It should be noted, however, that Jordan & Rothschild were not referring to the specimen herein described as *arcuata* when mentioning material from Korinchi, Sumatra, even though the slide of the unique holotype had been identified as *robinsoni* at the Rothschild Museum at Tring. The Korinchi specimens from "Benkulen, Sumatra," mentioned in 1922 were from "Padang Bovenlanden," not from the type locality of *arcuata*, although they were likewise collected by E. Jacobson in July, 1916. It seems to me that the omission of this specimen from the cited records was deliberate and that Jordan & Rothschild realized that it was not really *robinsoni*.

M. robinsoni has not been fully described or illustrated to date, although Traub (1951) figured the spermatheca and aedeagus and referred to it when diagnosing another species of *Stivalius s. lat.*

The species is somewhat variable throughout its range in the Malayan peninsula, although the differences are sufficiently minor to be considered as individual or artificial, e.g., due to the position of the spermatheca or the movable finger, etc., in the mounted specimen. There seems to be no valid evidence of subspeciation in the material extant, ranging from northern Malaya to Johore. The type specimen of *robinsoni*, unfortunately a female, is indistinguishable from material from Selangor. For these reasons, I feel that the Malayan slides represent the nominate form even though males from the "Thai Malay States" are unknown. Further, zoogeographic data also indicate that the major faunal differences between Thailand and Malaya, at least insofar as concerns rodents and fleas, occur substantially further north. Moreover, certain Malayan rat-fleas, such as *S. klossi* (Jordan & Rothschild, 1922) and

Neopsylla dispar Jordan, 1932, range much further north without apparent subspeciation (although distinct subspecies of *S. klossi* occur in the Indo-China region and in southern China).

However, there are significant differences between males from peninsular *M. robinsoni* and those on Java, Sarawak and even Tioman Island, off the east coast of Malaya, and such subspecies are described below. There is insufficient material at hand to treat Sumatran forms, although I believe that at least one subspecies occurs on that island as well. New subspecies are described after the diagnosis of the nominate form.

4a. **Medwayella robinsoni robinsoni** (Rothschild, 1905)

Diagnosis. (1) Thumb (figs 23, 44, THM.) of alpha-portion (ALPH.) with apical margin only slightly longer than height of structure. (2) Upper arm (U.A.) of securifer with free "snout" about 3·3 times as long (measured from vertical internal root) as broad at middle. (3) Lower arm (L.A.) relatively broad; about 1·2 times as long (measured from level of apex of pivotal chord, PIV.CD.) as broad at middle; dorsal margin plunging ventrocaudad at basal $\frac{1}{3}$ or $\frac{1}{2}$ at an angle of about 60°, but margin mildly sinuate and distally slight recurved, apex blunt, not acuminate. (4) Quasi-crochet (Q.C.) with tanned portion about 4 times as long as broad. (5) Distal arm of sternum 9 (figs 1, 47, D.A.9; fig. 21) with apical lobe (AP.L.) fairly deeply sinuate, its upper half (qq–pp) quite convex; lower lobe (pp–oo) somewhat sinuate. (6) Notch (NCH.) of D.A.9 asymmetrical, lower margin (mm–nn) longer than upper margin (oo–nn); axis of notch (nn–rr) sloping ventrocephalad. (7) Female sternum 7 (fig. 49) with dorsal lobe (above ventral sinus) flattened or very shallowly concave, but lacking distinct sinus. (8) Ventral lobe of 7 S. with caudal (single) bristle usually equidistant from pair immediately cephalad, or with caudal bristle at most only somewhat closer to ventral member than dorsal member. (9) Dorsal wall of vagina (fig. 32, VAG.) caudad to glandula vaginalis (G.VG.) with 1 or 2 small knot-like or bead-like glands, 1 at about proximal $\frac{1}{4}$ and second usually near midpoint; wall fairly well tanned to near apex, at genital aperture.

Illustrations

1. Clasper and sternum 9
2. Preantennal region (♂)
17. Processes of clasper
21. Distal arm of sternum 9
23. Apical region of aedeagus
28. Sternum 8 (♂)
32. Internal genitalia (♀)
44. Apex of aedeagus
46. Apical region of aedeagus
47. Clasper and sternum 9
48. Transverse suture, D.A.9
49. Sternum 7 (♀)
50. Lateral metanotal area (♂)
51. Anal segments (♀)
52. Spermatheca
59. Genitalia and anal lobes (♀)

Comment. As shown in Table 3, the nominate, mainland form of *M. robinsoni* may be found on virtually any kind of squirrel, rat or tree-shrew in its forest-habitat. The majority of the specimens are from squirrels—*Callosciurus* or *Sundasciurus*, while *Tupaia* was also commonly infested. In general, then, the bulk of the specimens came from mammals that spend much or most of their time in trees, rather than from ground-squirrels. As indicated above, *M. r. robinsoni* is broadly distributed throughout Malaya, and we collected it in all surveyed forested areas which were not coastal, ranging from elevations as low as 100 ft up to as high as 6000 ft. The species was rare above 5000 ft and I believe that the existing records represent recent introductions of *C. caniceps* into regions cleared of forest by man, as at the top of Mt. Brinchang or along roadsides to such high elevations. Thus, we failed to collect either *C. caniceps* or *M. r. robinsoni* on Mt. Brinchang in 1948 and 1950, before a road was cut to the summit and a radio station constructed there. When we next collected there, in the period 1955 and thereafter, *C. caniceps* was fairly common in secondary forest and on the fringes. However, more data are required to clarity this point.

It is worthy of note that *M. robinsoni* was never collected in the coastal areas of Malaya nor on the islands off the west coast, i.e., Pangkor, Sembilan I. and Langkawi I.—and neither was any other species of indigenous flea. Over 50 specimens of *Callosciurus* and hundreds of rats were examined from the coastal mainland or Langkawi (no squirrels were found on Pangkor or Sembilan I.). The only squirrel collected on Langkawi was *C. caniceps*, and specimens were shot at elevations as high at 2000 ft, and no fleas were ever noted. However, at such altitudes, the samples checked were too few to warrant conclusions on the presence or absence of *Medwayella* and other fleas. These points are discussed further, below, after the description of new species, etc.

4b. **Medwayella robinsoni peregrinata** subsp. nov.

TYPE MATERIAL. Holotype ♂ (B-48232) ex *Callosciurus notatus*; EAST MALAYSIA: W. Sarawak, Pueh; 3.VI.1958; Coll. T. C. Maa. Allotype ♀ (B-49372) ex *C. notatus*; Sarawak, (3rd Division), Bruit Isle, Rajang Delta; 22.VII.1958; Coll. T. C. Maa. Paratypes as follows: 1 ♂, 1 ♀ with same data as allotype; 2 ♂ ex *C. notatus*; S.W. Sarawak, Tapuh; 9.VII.1958; Coll. T. C. Maa. Holotype, allotype in U.S. National Museum, with holotype bearing number U.S.N.M. number 71599. Paratypes in collection of B. P. Bishop Museum (Honolulu) and that of author.

DIAGNOSIS. (1) Labial palpus extending to just beyond base of pro-trochanter instead of to (or near) apex of procoxa as in other subspecies. (2) Distal arm of sternum 9 (fig. 55) with apical lobe (AP.L.) appearing at first glance to be largely truncate, but actually upper portion (fig. 1, pp–qq) convex, and only lower, longer portion (oo-pp) quite straight. In the nominate form (fig. 47, D.A.9 and fig. 21) the 2 portions are subequal and oo–pp is concave. (3) Lower arm (fig. 57, L.A.) of securifer generally somewhat acute apically, primarily due to the fact that ventral margin is straight to near apex, instead of being sinuate and upcurved subapically (figs 23, 44) so that the tip is broadly angled. (4) Tanned portion of quasi-crochet (Q.C.) about 3·5 times as long as broad at middle, not 4 times.

Similar to the nominate form in other respects, including F., and even the details of the internal female genitalia.

ILLUSTRATIONS

55.	Distal arm of sternum 9	60.	Spermatheca and sternum 7
57.	Apex of aedeagus	61.	Genitalia (♀)

COMMENT. It may be significant that there are no records of *M. robinsoni* from North Borneo, where 4 other species of *Medwayella* are known to occur, and where members of the type-host, *C. notatus*, were examined for fleas, in one locality, namely Mt. Kinabalu at 5000 ft elevation or higher. However, even where present, *M. robinsoni* is rare at such altitudes (at least in Malaya). There have been too few collections from the foot-hills and coastal areas of North Borneo to provide adequate data in regard to the possible occurrence of *M. robinsoni*. Since this species is so widely distributed in Sarawak, one would expect a similar distribution in N. Borneo, if it were present at all, but as mentioned below in the section on zoogeography, the flea fauna of North Borneo may be significantly different from that of at least southern Sarawak.

The subspecies name is derived from the Latin word *peregrinor*, meaning to travel abroad, and was selected to emphasize the distance between the mainland nominate form and the Bornean subspecies in terms of space, if not geologic time. However, it is not necessarily implied that the spread of *M. robinsoni* or of its hosts, through the eons, was from Malaya to the islands. This point is discussed in the third paper in this series and which deals with zoogeography.

4c. **Medwayella robinsoni bogora** subsp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-78347-1) ex *Callosciurus notatus*; INDONESIA: Java, Bogor; elev. 260 m; 15.VII.1965; Coll. J. M. Stusak. Paratypes as follows: 16 ♂, 17 ♀ with same data as holotype, but collected 21.VI.1965–2.II.1966. 2 ♂, 1 ♀ ex *C. nigrovittatus*; loc. cit.; 21.VI.1965. 1 ♀ ex *Petaurista elegans*; Tjibodas; 2.X.1965. 1 ♂, 4 ♀ ex *Lariscus insignis*; loc. cit.; 3.X.1965. All collected by J. M. Stusak. Holotype and allotype deposited in U.S. National Museum, with holotype bearing U.S.N.M. number 71600. Paratypes in collections of B. P. Bishop Museum (Honolulu), that of author, and other institutions listed for *M. dryadosa* above.

DIAGNOSIS. Immediately separable from the nominate form and the new subspecies herein described in that notch in distal arm of sternum 9 (fig. 54, NCH.) is nearly symmetrical, i.e., lower margin (cf. fig. 1, mm–rr) is only slightly longer than upper (oo–rr) instead of being distinctly shorter (fig. 21). Equally characteristic is the fact that axis of notch (nn–rr) parallels the long axis of the body instead of inclining ventrocephalad. Further distinguishable from *M. r. robinsoni* as follows: (1) Height of thumb (fig. 58, THM.) of alpha-portion of Ford's sclerite about twice as broad (long) apically as high and thus not nearly as tall as in nominate form (figs 23, 44), where THM. is nearly as high as long. (2) Upper arm (U.A.) of securifer with free "snout" relatively shorter and stouter, about 2·5 times as long (measured from vertical internal root) as broad at middle, instead of 3·3 times. (3) Apical lobe (AP.L.) of D.A.9 with upper portion (cf. fig. 1, pp–qq) oblique, not convex. (4) Lacking bead-like sclerotizations on dorsal wall of vagina (fig. 62, VAG.), distad of glandula vaginalis (G.VG.). (5) With only 2 bristles on ventral lobe of sternum 7 (7 S.), not 3. (6) Female often with a "supernumerary" bristle between rows II and III of head; this is unusual in mainland *M. robinsoni* (the nominate form). Very similar to the nominate form in other essential respects.

ILLUSTRATIONS

54.	Distal arm of sternum 9	62.	Spermatheca, genitalia and sternum 7
58.	Apex of aedeagus	63.	Proximal arm of sternum 9

COMMENT. The known specimens were primarily all from *Callosciurus notatus*, but it is anticipated that this subspecies also commonly occurs on *C. nigrovittatus*. The data, although inadequate, also suggest that, like the nominate form, *M. r. bogora* readily infests other squirrels, etc., in its habitat. The name *bogora* should be regarded as a coined term, although suggested by the type-locality, Bogor.

4d. **Medwayella robinsoni tiomanica** subsp. nov.

TYPE MATERIAL. Holotype ♂ (B-55344-1) ex *Callosciurus nigrovittatus*; WEST MALAYSIA: Pahang, Pulau Tioman, on Kampong Tekek-Kampong Juara Track; elev. 500 ft; 30.III.1962; Coll. Ng Cheong Kee et al. Allotype ♀ (B-55335) ex *C. notatus*; loc. cit., but Kampong Tekek; 18.III.1962. Paratypes (all collected by Ng Cheong Kee et al. in 1962, unless otherwise indicated) as follows: 2 ♂ with same data as holotype. 2 ♂, 3 ♀ ex *Sundasciurus tenuis*; loc. cit. but 20.III. 3 ♂, 3 ♀ ex *Tupaia glis*; loc. cit. but elev. 150-500 ft; 20-23.III. 2 ♂ ex *Lariscus insignis*; loc. cit. but elev. 150 ft; 22.III. 3 ♀ with same data as allotype but 18-19.III. 1 ♂, 2 ♀ ex *C. nigrovittatus*; loc. cit. 3 ♂, 1 ♀ ex *T. glis*; loc. cit. but 2.V.1966; Coll. M. Nadchatram. 1 ♀ ex *L. insignis*; loc. cit. but 1.V.1966; Coll. M. Nadchatram. 7 ♂, 3 ♀ ex *Iomys horsfieldi*; Kampong Juara; elev. 150 ft; 25-31.III. 2 ♂, 2 ♀ ex *S. tenuis*; loc. cit. but 11.IV. 10 ♂, 4 ♀ ex *T. glis*; near camp; elev. 50-1000 ft; 8-9.IV. 1 ♂ ex *Rattus t. tiomanicus*; loc. cit. but elev. 500 ft; 9.IV. 5 ♂, 4 ♀ ex *T. glis*; Ulu Sungei Ayer Besar; elev. 800-900 ft; 9-11.IV. 1 ♂ ex *L. insignis*; loc. cit. but elev. 900 ft; 10.IV. 1 ♂, 1 ♀ ex *R. sabanus*; loc cit. but 11.IV. 2 ♂, 1 ♀ ex *T. glis*; Kampong Mokut; 9.IV. 1 ♂ ex *L. insignis*; Ulu Lelang, 17.IV. 1 ♀ ex *R. surifer*; loc. cit. but 16.IV. 1 ♂ ex *C. notatus*; Pulau Tulai, 6 mi NW of Pulau Tioman; 4.IV. 1 ♂, 1 ♀ ex *C. notatus* nest; loc. cit. Holotype (U.S.N.M. No. 71601) and allotype deposited in U.S. National Museum. Paratypes in that institution, the British Museum (Natural History), B.P. Bishop Museum (Honolulu), University of Malaya and Institute for Medical Research (both Kuala Lumpur) and the author's collection.

DIAGNOSIS. (1) Apical lobe (fig. 53, AP.L.) with upper portion (cf. fig. 1, pp–qq) rather oblique and straigt instead of being convex as in the nominate form (fig. 21, 47); not nearly as vertical as in *M. r. peregrinata*. (2) Thumb (fig. 56, THM.) of alpha-portion of Ford's sclerite with stem shorter than nominate form, the untanned vertical portion definitely shorter than distal breadth, instead of only slightly so. (3) Lower arm (L.A.) of securifer with free portion proportionately longer and narrower than in mainland form e.g., length (measured from level of apex of pivotal chord, PIV.CD.) about 1·5 times as long as high at that level, not merely 1·2 times. Relative narrowness of extended part of L.A. applies to apical excised region as well as proximal section. (4) Lacking bead-like sclerotizations on dorsal wall of vagina (fig. 64, VAG.) distad to glandula vaginalis (G.VG.) which are characteristic of the nominate form. (5) Ventral lobe of sternum 7 (7 S.) subequal to lobe above it, instead of being definitely larger.[5]

ILLUSTRATIONS

53. Distal arm of sternum 9
56. Apex of aedeagus
64. Spermatheca, genitalia and sternum 7

COMMENT. *M. r. tiomanica* infests a variety of squirrels and small mammals of similar habit and habitats in the forest on the hills of Tioman Island, primarily *Tupaia* and tree-squirrels, thereby paralleling the mainland form.

5. **Medwayella phangi** sp. nov.

TYPE MATERIAL. Holotype ♂ and allotype ♀ (B-46948-1) ex *Sundasciurus tenuis*; WEST MALAYSIA: Selangor, Subang; elev. 500 ft; 30.X.1957; Coll. R. Traub. Paratypes (48 ♂, 19 ♀) as summarized in Table 1 (p. 216). Holotype (U.S.N.M. number 71602) and allotype in collections of U.S. National Museum. Paratypes distributed as for *M. dryadosa*.

DIAGNOSIS. Male instantly separable from *M. dryadosa* and *M. robinsoni* in that dorsal margin of distal arm of ♂ sternum 9 is apically homolate (uniformly flat) (fig. 68, HOM.) terminating in an apical nubbin or short claw, instead of bearing a distinct subapical notch (fig. 20, NCH.) and an apical truncate or sinuate lobe (fig. 21, AP.L.). Further distinguishable from these species in that :(1) Quasi-crochet (fig. 71, Q.C.) is narrowed, elongate, its length, measured along entire ventral margin, more than 2·5 times length of base of phylax (PHY.) and upcurved; instead of being of quite uniform breadth, straight and short (at most only somewhat longer than base of PHY.), (figs 22, 23, Q.C.). (2) Dorsal region of Ford's sclerite characterized by a groove-like process (fig. 71, GRV.) formed by the close appression of the inner faces of the anterior portions of alpha-portion (ALPH.) and elongated base of upper arm (U.A.) of securifer, the tanned and parallel margins creating the effect of an open tube. *M. dryadosa* and *M. robinsoni* with Ford's sclerite lacking narrow groove; and instead apex of alpha-portion is thumblike (figs 22, 23, THM.). (3) Deltoid flap (DEL.FL.) very narrow due to great depth and height of sinus in hood, which extends far cephalad and hence exposing apex of phylax (PHY.) and body of crochet (B.CR.), instead of being broad and covering all of apical sclerites except tips of securifer (U.A. and L.A.) and crochet process (CR.P.). (4) Pivotal chord (PIV.CD.) well tanned and upcurved caudally instead of being lightly sclerotized and straight. (5) Movable finger (figs 65, 66, F.) with distal fringe of bristles (D.FR.) with bases of upper 4 in a straight line, and caudal margin also straight here, instead of line of bases of D.FR. and adjacent caudal margin each forming an arc (figs 14, 17). (6) Margins of F. below D.FR. fairly strongly curved and subparallel to near apex of immovable process P. (level r–s in fig. 1, *q.v.* and *cf.*) not with a slight curve to F. and margins diverging at midline so that both are rather convex at level of conical process

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[5] If the specimen has been distorted in mounting, one side may appear larger than the other. Both sides should be similar in appearance before interpretations are made.

(C.P.) (i–q). (7) Male sternum 8 (fig. 69) with distinct microtufts on caudal ⅓ or ¼ of ventral margin; not microdenticulate (fig. 29, s3–t3). (8) Upright portion (bb–ff) of dorsal (proximal) arm of sternum 9 mainly convex; not flat as in *M. dryadosa* (fig. 18, P.A.9). (9) Upper lobe of ♀ sternum 7 (figs 75, 76, 7 S.) slightly concave above subventral sinus, not convex (figs 26, 49). (10) Perula of bursa copulatrix (fig. 77, P.B.C.) long and mainly vertical, e.g., vermiform, its caudal margin well tanned and resembling a shallow, straight arc; sac of B.C. (SAC.) dilated and long (sausage-shaped) paralleling it; instead of P.B.C. being short and oblate-ovate and SAC. quadrate above and behind it (figs 31, 32). (11) Paragenital morion (PG.M.) well developed, several times longer and broader than glandula vaginalis (G.VG.); not merely subequal to it.

Near *M. rhaeba* (figs 138, 139) from Mt. Dulit, Sarawak, and known only from 1 pair and agreeing with it as follows: (1) With a groove-like process (fig. 71, GRV., *M. phangi*) on Ford's sclerite. (2) Upper arm (U.A.) of securifer (SEC.) relatively long and narrow. (3) Quasi-crochet (Q.C.) long, subapically narrowed and upturned. (4) Distal arm of sternum 9 (fig. 69) lacking a subapical notch; dorsal (anterior) margin rather flat (HOM.) between apex and subapical lobe (SUB.L.). (5) posterior region of ventral margin of ♂ sternum 8 microtufted (fig. 69, 8 S.). (6) Female sternum 7 (fig. 76) shallowly concave above subventral sinus.

Markedly differing from *M. rhaeba* as follows: (1) in new species, constricted portion of movable finger (fig. 66, F.) below distal fringe (D.FR.) (e.g., region marked j–k in fig. 1) almost as broad as region above it, whereas in *M. rhaeba* (fig. 138) j–k is ½ width of apex (l–p). (2) Caudal margin of F. only somewhat convex at level of apex of P. (r), its breadth here equal to less than ½ length of F. above P. (n–s); not so grossly convex that breadth equals more than ½ of n–s. (3) F. so little curved that caudal margin below D.FR. is shallowly concave, instead of being so strongly arched that dorsocaudal angle (tip of stiva) (p) is in a plane with ventrocaudal tip of fulcral sclerite (F.S.) (a3). (4) The pair of longish thin bristles on caudal margin of F. well distad of the middle of sinus, closer to D.FR. than to apex of P., instead of being closer to P. than to D.FR. as in *M. rhaeba*. (5) Apical margin of distal arm of ♂ sternum 9 (fig. 68) flattened (qq–ss) and tip (qq) extending slightly as a short, straight nubbin, whereas in *M. rhaeba* the top is somewhat convex and bears a distinct tooth-like projection (qq) which is somewhat curved (fig. 138). (6) Upcurved, narrowed portion of quasi-crochet (fig. 71, Q.C.) shorter, its length (measured along ventral margin) much less than distance from base of process to ventral angle, instead of slightly exceeding it. (7) Upper arm (U.A.) of securifer slightly arched in new species, not straight. (8) Sinus near ventral margin of ♀ sternum 7 (fig. 76, 7 S.) more acute than in *M. rhaeba*, making an angle of about 23° with horizontal, not 30° (fig. 139). (9) Tergum 8 of ♀ (fig. 77, 8 T.) with a lobe at ventrocaudal angle; this apparently lacking in *M. rhaeba*.

Readily separable from *M. javana* and *M. arcuata* by the characters cited as numbers 1–4 above in comparison with *M. dryadosa* and *M. robinsoni*. Further distinguishable from *M. javana* by the following: (1) F. fairly broad subapically (fig. 66), breadth immediately below D.FR. (j–k) being almost ⅘ of length from this level to apex (j/k–n) instead of being narrow, less than ½ of length above it, as in *M. javana* (fig. 133). (2) Quasi-crochet (fig. 71, Q.C.) more than twice as long as base of phylax (PHY.) instead of only slightly longer (fig. 95). Distingiushable from *M. loncha* at a glance, viz., (1) D.A.9 (fig. 67) lacking conspicuous spur (mm) at middle of anterior (dorsal) margin (fig. 127). (2) Quasi-crochet (fig. 71, Q.C.) long and narrow, about thrice as long as broad at base instead of being short and broad, only about twice as long as broad (fig. 128).

DESCRIPTION. Essentially as in *M. dryadosa* except as noted in diagnosis above and as follows: Mesepisternum with lobe at cephaloventral corner virtually straight.

Male. Lumacaudate process (fig. 69, LUM. and fig. 70) not as well developed—viz., lateral apical seam or flap inapparent; process shorter, apically more narrowed and not as heavily armed with spiniforms, either in number or regarding modification, i.e., with only 5–6 transverse rows of short, stout, slightly curved bristles of subspiniforms which are well separated from one another, instead of 12–16 rows of close-set modified bristles of which apical and ventral ones, especially, are true spiniforms (i.e., short, dark, basally widened, curved and broad to near pointed apex, etc., as in fig. 12); LUM. subapically only about ⅗ as broad as near base instead of being subequal. Male with upper antepygidial bristle only ⅓ length of lower one. Distal arm of ♂ sternum 9 with supramedial flap (fig. 69, SUP.FL.) possessing fairly short and weakly sclerotized thickening (THK.) on base, and that is apical. SUP.FL. extending to apex of D.A.9. Dorsal (upper) margin of securifer, i.e., basal ½ of upper arm (fig. 71, U.A.) concave so that entire structure is biconcave dorsally; free portion of U.A. with basal axis somewhat upcurved (about 40° from axis of base). Lower arm (L.A.) apically truncate but lower angle rather acuminate and with tip usually recurved and hence often obscured. Ventral margin of base of S.I.T. broadly convex to level of dorsal triangular thickening (which is not spur-like) at apical third. Apex of S.I.T. with ventral margin extended caudad. Phylax (PHY.) nearly twice as high as broad at base. Quasi-crochet (Q.C.) somewhat boomerang-shaped; ventral angle rounded; proximal portion slightly exceeding distal; broadest at angle; upturned distal portion with ventral margin shallowly concave; upper margin curving at distal ¼ so that apex is ovate dorsally. (Note—Caudomarginal submedian group of bristles, CM.G.B., on D.A.9, usually with 3 stout bristles, not 2 as in specimen drawn in figure 68.)

Female. Sternum 7 (figs 76, 77, 7 S.) with ventrocaudal lobe somewhat too long and broad to be an inverted, reversed image of sinus above it. Mesal genitalic ridge of 8 T. (figs 72, 77, M.R.8) consisting of a broadly crescentic sclerotization with short, broad, sinuate tail extending caudad and an indefinite tanned stalk arising from ventral base of crescent. Sternum 8 relatively broad, length distad to level of basal (most anterior) bristle subequal to breadth of segment at that level (or shorter), with about 4–6 bristles of which all but 1 of apical ones are dorsal and subapical; lower apical bristle the longest, but this shorter than twice breadth of 8 S. at level of basal bristle. Spermatheca (figs 74, 77) with dorsal constriction nearer to middle than to caudal ⅓; bulga (B.) about 2·4 times as long (middle longitudinal axis) as broad at constriction; dorsal peak on caudal bulge short, inapparent unless spermatheca seen in full lateral aspect. With internal sector of hilla (H.) shorter than external portion.

Sac of bursa copulatrix (SAC.) an indefinite, long, tubular, dilated, sausage-like structure about 3–4 times as broad as diameter of B.C. near orifice to vagina. Spermathecal duct (D.SP.) with dilated portion (DIL.P.) equal to diameter of SAC. and then gradually narrowing so that at middle its diameter is $\frac{1}{2}$ that of DIL.P. and anterior $\frac{1}{3}$, about $\frac{1}{8}$. Perula (P.B.C.) usually subvertical and quite straight except for cephalad gradual curve of extremities, or else resembling a flattened arc with concavity anterior. Glandula vaginalis (G.VG.) a straight but oblique tanned slit, about thrice height of small accessory "gland" between it and unmodified orifice of B.C. Dorsal wall of vagina well developed caudad of G.VG. and here with marginal striae or bands. Paragenital morion (PG M.) highly developed, consisting on each side of a tube-like coil surrounding all but the rear of an ovoid lightly tanned core, and occupying most of the region between P.B.C. and lower part of sternum 9 (9 S.).

ILLUSTRATIONS

66. Processes of clasper
68. Distal arm of sternum 9
69. Sternum 8 (♂)
70. Lumacaudate process
71. Apical region of aedeagus
72. Tergum 8 (♀)
73. Anal lobes and stylet (♀)
74. Spermatheca
76. Sternum 7 (♀)
77. Spermatheca, genitalia and anal segments

COMMENT. The species is named for Phang Ong Wah, who has faithfully served USAMRU (Malaya) as a collector and careful observer of small mammals and ectoparasites in Malaya, North Borneo and Sarawak since 1948, despite the arduous labor and physical danger (from both disease and hostile guerillas) that the field-work often entailed. Mr Phang was responsible for the collection of many of the specimens and new species of fleas and trombiculid mites studied by the writer, and also contributed significantly to our investigations on the chemoprophylaxis, treatment, control and ecology of scrub typhus.

A distinctive subspecies of *M. phangi* occurs in Sarawak and the nominate form will therefore be characterized before the description of the Bornean one, and before a discussion of the host-relationships and distribution of the Malayan form.

5a. Medwayella phangi phangi

DIAGNOSIS. (1) Movable finger (fig. 66, F.) with distance between basal bristle of distal fringe (D.FR.) and apex of F. subequal to breadth of F. at subapical constriction. (2) Concavity of caudal margin of F. shallow; this arc with its chord about 9 times its height. (3) D.A.9 (fig. 68) with homolate margin (HOM.) relatively long in that the slope of the subapical lobe (SUB.L.) is fairly abrupt, terminating at basal $\frac{1}{5}$ of distance between apex of SUB.L. and tip of D.A.9 (mm–qq in fig. 1). (4) Distance mm–qq scarcely exceeding that between apex of SUB.L. and distal margin of median microspiculose area (M.MSP.) (mm–kk). (5) Sinus above ventral lobe of ♀ sternum 7 (fig. 76, 7 S.) subequal to lobe beneath it. (6) Paragenital morion (fig. 77, PG.M.) with a thin transverse sclerotization across anterior portion of core.

HOST-RELATIONSHIPS AND DISTRIBUTION AND OTHER COMMENTS. It is noteworthy that more than 90% of Malayan *M. p. phangi* (the nominate form) were from

Tupaia glis or *Sundasciurus tenuis* or *S. lowi* and that there were only 2 records from any of the truly arboreal squirrels (Table 2, p. 259), and only 1 specimen was found on a rat, even though the *Callosciurus* and *Rattus* constituted the largest categories of hosts examined. The absence of *M. p. phangi* from *Dremomys* and *Rhinosciurus* and the dearth of records from *Lariscus* is also striking.

The geographic and ecological distribution of this flea in Malaya is unusual and merits further study, but available data are summarized in Table 1 (p. 216). Although over the years since 1947, both USAMRU and DMZ-IMR collected mammals and fleas more intensively in the dipterocarp forest in the foothills around Kuala Lumpur (i.e., the forest reserves at Gombak, Ampang, Ulu Langat and Bukit Lagong areas) than in any other region or habitat, only 4 specimens of *M. p. phangi* were ever found there. In contrast, 27% of the specimens (and 30% of the numbers of collections, i.e., the hosts infested with *M. p. phangi*) were made from the secondary forests of Subang, which is also in Selangor and equidistant from Kuala Lumpur with the other areas, but at slightly lower elevation (viz., 400–700 ft versus 1000–2000 ft). Further, 40% of the specimens (35% of the collections) were from the foothills of Perak, 8–10 miles from Ipoh at elevations of about 1100 ft. This would at first glance suggest that the distribution might be an altitudinal one, a possibility that is reinforced by the absence of records from montane hosts like *Dremomys* and *Tamiops mcclellandi*. However, *M. p. phangi* is not really a lowland species, because 15% of the specimens came from Kedah Peak, at elevations often above 3000 ft, an area where relatively little collecting of ectoparasites was done by our teams and colleagues.

One likely explanation is that *M. p. phangi* is essentially a flea of secondary or disturbed forest, rather than primary forest, for all of the sites where it has been taken in reasonable numbers are regions where there has been much cutting of timber over the years or where there is an abundance of limestone formation and a dearth of the huge dipterocarps associated with primary forest in Malaya. The forest reserves of Selangor, on the other hand, have been much less altered by man, and the areas surveyed were not in limestone terrain. Another factor worth checking is that of rainfall, for the Perak and Kedah Peak collections happened to have been made during periods of relative drought. The one-to three-week dry-spells noted annually or semi-annually in most of the southern two-thirds of Malaya do not occur at fixed periods of the year, and no special effort was made to collect *Tupaia* and *S. tenuis* in the dipterocarp forest during those irregular periods. Hence data are lacking whereby this point could be determined regarding the forested belts in Selangor.

However, the distribution of *M. p. phangi* may prove to be due to zoogeographic factors, for like another new species described below and known only from west-central Malaya, it occurs in Sarawak as a distinct subspecies. Definite faunal relationships may exist between these two regions, as mentioned anon, and as discussed in the third paper in this series.

Further discussion on the host-relationships of *M. p. phangi* will be found in the comments following the descriptive sections on *Medwayella*.

M. p. phangi also occurs in extreme southern Thailand (Nakhon Si Thammarat), where a single female was collected on an unidentified squirrel by Dr Boonsong

Lekagul and kindly sent to us by Dr R. E. Elbel. It seems significant that no additional specimens of *M. phangi* turned up in the rather extensive collections of fleas made in Thailand by Dr Elbel, for the vast majority of Elbel's Thai specimens were taken north of the Malayan peninsula. In these "non-Malayan" provinces of Thailand, a new species of *Medwayella*, described later in this paper, was commonly found on *Menetes berdmorei*, a ground-squirrel and it is of interest that this new species was also taken at Nakhon Si Thammarat.

5.b **Medwayella phangi tana** subsp. nov.

Type material. Holotype ♂ (B-48275-1) and allotype ♀ (B-48275-3) ex *Tupaia tana*; EAST MALAYSIA: W. Sarawak, Pueh; 11.VI.1958; Coll. T. C. Maa. Paratypes as follows: 5 ♂, 5 ♀ with same data as holotype. 1 ♂ ex *Callosciurus*; loc. cit. 5 ♂, 6 ♀ ex *T. tana*; Sarawak, Kuching, 5th mile, Stapok Rd.; IX.1951; Coll. T. Harrison. Holotype (USNM number 71603) and allotype in collection of U.S. National Museum. Paratypes in B. P. Bishop Museum (Honolulu), the British Museum (Natural History) and the author's collection.

Diagnosis. Close to nominate form, and differentiated as follows: (1) Movable finger (fig. 65, F.) narrower and more arched below distal fringe (D.FR.), viz., fringe set on a low "stalk" in the Sarawak form—breadth of F. at constriction (indicated as j–k in fig. 1) much shorter than distance between basal bristle of fringe and apex of F. instead of being subequal; the arc formed by caudal margin of F., e.g., between D.FR. and where margin crosses apex of immovable process P. (k–r) quite deep, e.g., with chord equal to 4·5 times of altitude, instead of about 9-fold. (2) Apex of D.A.9 (fig. 67) with homolate margin (HOM.) comparatively short because slope of subapical lobe (SUB.L.) commences at basal ⅓ of distance between tip of SUB.L. and apex of D.A.9 (mm–qq), instead of basal ⅙ (fig. 68). Distance mm–qq nearly twice that between apex of SUB.L. and distal margin of median microspiculose area (M.MSP.) (mm–kk) instead of scarcely exceeding it. (4) Sinus above ventral lobe of ♀ sternum 7 (fig. 75, 7 S.) definitely shorter and narrower than lobe below it, instead of being subequal (fig. 76, 7 S.). Paragenital morion with a tanned chord along ventral margin of inner core, near its apex. In nominate form there is instead a thin transverse sclerotization curving towards middle of or dorsal part of core (fig. 77, PG.M.).

Illustrations

65. Processes of clasper
67. Distal arm of sternum 9
75. Sternum 7 (♀)

Comment. The name of the subspecies denotes a common host, *Tupaia tana*, as per existing records. However, collections in Sarawak have been too limited in general to determine whether the Bornean subspecies regularly infests ground-squirrels or other hosts.

6. **Medwayella limi** sp. nov.

Type material. Holotype ♂ (B-45230) ex *Rhinosciurus laticaudatus*; WEST MALAYSIA: Selangor, Kepong, Bukit Lagong; 25.VII.1956; Coll. R. Traub.

Allotype ♀ (B-52520) ex *R. laticaudatus*; Selangor, Ampang Reservoir; 13.I.1960; Coll. J. R. Audy. Paratypes as follows: 4 ♂ with same data as holotype. 2 ♂ ibid., but 31.X.1956. 1 ♂ with same data as allotype. 2 ♂ ibid., but 16.VIII.1960; Coll. J. R. Audy. 10 ♂, 2 ♀ Selangor, Ulu Langat Forest Reserve; 21.I–18.II.1965; Coll. Lim Boo Liat. 1 ♂ ibid., but 15.I.1957; Coll. R. Traub. 3 ♂, 1 ♀ Selangor, Ulu Gombak Forest Reserve, 16–17 mi N of Kuala Lumpur; 22.VIII, 4.X, 16.XII.1956; (R.T.). 1 ♂ ibid., but 30.IX.1968; (L.B.L.). 2 ♂ Selangor, Pahang Road, 16 mi N of Kuala Lumpur; 5.VII.1948, 7.III 1956; (R.T.). 4 ♂, 1 ♀ Trengganu, Sungei Tong Forest Reserve; 26.VIII.1965; (L.B.L.). 2 ♂ ex *Lariscus insignis*; Selangor, Ulu Gombak, 15–16 mi N of Kuala Lumpur; 1500 ft elev.; 22.VII.1957, 11.VI.1958; (R.T.). 1 ♂ Trengganu, Bukit Besi; 5.VIII.1958; (R.T.). 1 ♂ ex *Tupaia glis*; loc cit. 1 ♀ ex *Rattus sabanus*; Selangor, Ampang Reservoir; 28.VII.1960; (R.T.).

Holotype (U.S.N.M. number 71604) and allotype deposited in U.S. National Museum. Paratypes distributed as for *M. dryadosa*.

DIAGNOSIS. Very close to *M. phangi* but distinguishable as follows: (1) Groove-like process of Ford's sclerite (fig. 82, GRV.) incomplete apically due to fact that thickened ventral margin of base of upper arm (U.A.) does not extend as far dorsally as does the opposite member of the furrow, and instead terminates well before apex. In *phangi* (fig. 71) the edges of the groove parallel each other all the way to apex. (2) Apex of anterior member of GRV. extending over and beyond (dorsad) base of U.A. as a broad, truncate and squared flap whose caudal margin parallels its anterior one, and which crosses base of U.A. at anterior ¼. In *phangi*, this flap does not reach dorsal margin of base of U.A. and its caudal margin is convex. (3) Free extension of U.A. (snout) more upright, making an angle of about 45° with longitudinal axis of base of U.A. instead of only about 20–25°. (4) Free portion of lower arm (L.A.) quite narrow subapically due to slope of 60° of upper (dorsal) margin and emargination of ventral one. In *M. phangi*, upper margin sloping at 80° and ventral margin straight to near apex. (5) Tongue-like apical portion of quasi-crochet (Q.C.) shorter, due to Q.C. being angled at apical ⅓ instead of near midpoint (fig. 71). (6) Phylax (PHY.) with base much broader; its height only less than 1·4 times length of ventral margin instead of nearly twice as high. (7) Subapical lobe (fig. 81, SUB.L.) of D.A.9 with its height equal to twice that of nubbin at apex (indicated as qq in fig. 1) and with homolate margin (HOM.) correspondingly shortened, e.g., flat surface between qq and mm shorter than breadth of D.A.9 at level of apex of M.MSP. (kk) instead of with SUB.L. about subequal to apical nubbin (figs 67, 68) and HOM. longer than D.A.9 is broad at level of kk. (8) Movable finger (fig. 80, F.) with bases of distal fringe of stout bristles (D.FR.) making an oblique line with longitudinal axis of F. (n–s), not a subparallel one (fig. 66). (9) Mesal genital ridge of ♀ 8 T. (fig. 79, M.R.8) with ventral arm longer, thinner and more discrete than in *M. phangi* (fig. 77), e.g., ventral tanned area clearly exceeding in length the more dorsal oblique sclerotization; and that of the median ovate ventral bulge. (10) Perula of bursa copulatrix (P.B.C.) with sclerotized caudal margin essentially straight or slightly concave (e.g., with sinus caudal) instead of being arched (convex dorsally) or with at least upper and lower fourths curving cephalad. (11) Paragenital morion (PG.M.) with a subventral sclerotization rather than a transverse one approaching dorsal margin. (12) Ventral lobe of sternum 7 (7 S.) taller than long, instead of with subequal dimensions. (13) Glandula vaginalis (G.VG.) 4 or more times length (height) of accessory "gland" (cleft) preceding it, not merely thrice as long.

In other respects *M. limi* is essentially like *M. phangi*. The diagnostic features cited under *M. phangi* serve to separate *M. limi* from *M. dryadosa*, *M. robinsoni*, *M. arcuata*, *M. loncha*, etc.

ILLUSTRATIONS

78.	Spermatheca (variation in aspect)	82.	Apex of aedeagus
79.	Spermatheca and genitalia	83.	Lumacaudate process
80.	Processes of clasper	84.	Spermatheca and genitalia
81.	Distal arm of sternum 9	85.	Sterna 8 and 9 (♀)

COMMENT. The species is named in honour of Mr Lim Boo Liat of the Division of Virus Research and Medical Zoology of the Institute for Medical Research, Kuala Lumpur, as partial acknowledgement of the tremendous assistance he has rendered the author and other members of USAMRU in their research on vectors and reservoirs of infection in Malaya and Borneo. Ever since 1948, Mr Lim not only collected mammals and ectoparasites with us or for us, but provided identification of hosts and served as major-domo, interpreter or liaison officer on innumerable field-trips and often under very difficult circumstances. Mr Lim also participated in Lord Medway's expedition to Gunong Benom, and, also, in his own right has contributed a great deal to the knowledge of the role of ectoparasites and small mammals in infections in Southeast Asia and in popularizing the study of natural history in that part of the world.

M. limi is a sibling species of *M. phangi* and it is of interest that the two species appear to differ significantly regarding host and habitat. Virtually all the records of *M. limi* are from the ground-squirrel *Rhinosciurus laticaudatus*, while the great majority of its sister-species were collected from *Sundasciurus tenuis* and *Tupaia*, and it was never found on *Rhinosciurus*. While nearly all of the *M. limi* were taken in the dipterocarp forests in the foothills near Kuala Lumpur, it probably is distributed in similar habitats throughout Malaya, since it was also collected in such terrain in Trengganu. There are no records from the lowland forest at Subang nor from the limestone hills of Ipoh, which were the main source of *M. phangi*. Both host-wise and with respect to micro-environment, *M. limi* resembles *M. dryadosa*, a point that is further discussed after the taxonomic portions of this article (p. 258 et seq.).

7. ***Medwayella thurmani*** sp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-15288) ex *Menetes berdmorei*; THAILAND: Nakhon Ratchasima, Si Khiu, Pak Chong; 23.IX.1952; Coll. R. E. Elbel. Paratypes, all from Thailand, as follows:

♂	♀	Host	Changwat & Locality	Date	Collector
15	8	*Menetes berdmorei*	Nakhon Ratchasima, Si Khiu, Pak Chong	IX.1952 & IX.1953	R. E. Elbel
1	–	*Rattus rajah* group	Nakhon Ratchasima, Si Khiu, Chan Thuk, Pongekeng	15.II.1953	R. E. Elbel
1	1	*Rattus rattus*	Nakhon Ratchasima, Pak Thong Chai	20.I.1967	J. F. Reinert
5	3	*Menetes berdmorei*	Nan, Pang Nam Un	19–21.I.1953	R. E. Elbel & H. G. Deignan
1	1	*Menetes berdmorei*	Nan, Sar Dist., 14 km S of Sarat Pahang	9.XII.1961	Phang Ong Wah
–	5	*Tupaia glis*	Nan, Ban Pha Hang	15–19.III.1961	K. Thonglongya
–	1	*Tupaia glis*	Loei, Dan Sai, Kok Sathon, Phu Lom Lo Mt., 2100 m	23.III.1954	R. E. Elbel & Boonsong Lekagul
3	1	*Menetes berdmorei*	Loei, same as above	29.III–2.IV. 1954	R. E. Elbel & Boonsong Lekagul
2	–	*Menetes berdmorei*	Loei, same as above	15.II.1955	R. E. Elbel
1	–	*Callosciurus finlaysoni*	Loei, same as above	17.II.1955	R. E. Elbel
3	5	*Menetes berdmorei*	Loei, Dan Sai, Na Haeo, Ban Na Muang, approx. 1780 m	9–27.X.1954	R. E. Elbel
5	2	*Tupaia*	Khon Khaen, 112–138 km on Khon Khaen–Loei Rd., 3–6 mi S of Loei Border	26.XI.–2.XII. 1962	R. Traub & J. E. Scanlon
–	1	*Menetes berdmorei*	Khon Khaen, 119 km on Khon Khaen–Loei Rd., 3 mi S of Loei Border	28.XI.1962	R. Traub & J. E. Scanlon
2	–	*Menetes berdmorei*	Chanthaburi, Klong Ta Kong, A Pong Nan Ron	22.II.1963	J. E. Scanlon
1	–	*Tupaia glis*	Chanthaburi, same as above	22.II.1963	J. E. Scanlon
–	7	*Rattus rattus*	Chanthaburi, Wad Bom Phu, A Tha Mai	21.II.1963	J. E. Scanlon
1	–	*Menetes berdmorei*	Chanthaburi, Khlung, Tapon, Khao Sabap Mt.	26.XII.1953	Boonsong Lekagul
1	–	*Tupaia glis*	Chiengmai, B. Nong Prue	15.XI.1965	D. Gould
2	–	*Menetes berdmorei*	Kanchanaburi, Trakhanum Hinlaem	9–25.XI.1952	R. E. Elbel & H. G. Deignan
–	1	*Menetes berdmorei*	Chon Buri, Si Racha, Khroa Wing	10.VII.1953	Boonsong Lekagul
–	1	*Menetes berdmorei*	Sara Buri, Kaeng Khoi, Muak Lek, Dan Kak Sat	8.IX.1953	R. E. Elbel
–	1	*Callosciurus notatus miniatus*	Nakhon Si Thammarat, Chawang, Chang Klang, Ban Na	28.II.1954	Boonsong Lekagul
2	4	*Tupaia glis*	Khao Yai National Park, Khorat	17–24.IX.1963	J. E. Scanlon

Holotype (U.S.N.M. number 71605) and allotype deposited in U.S. National Museum. Paratypes distributed as for *M. dryadosa*.

DIAGNOSIS. Distinctive in that apical portion of dorsal margin of distal arm of ♂ sternum 9 (fig. 91) lacks a distinct notch (fig. 47, NCH.) or a long and deep arc (fig. 33, ARC.) and yet is not evenly homolate (fig. 67, HOM.) from above subapical lobe (SUB.L.) to apex. Instead it bears a small, shallow arc (fig. 91, ARC.) proximally and a scarcely differentiated, longer apical lobe (AP.L.). Also separable from known species in the hyperdevelopment of sclerotized thickening (THK.) at base of supramedial flap (SUP.FL.) of D.A.9, which here extends from ventral region of ARC. to near apex of arm. Near *M. dryadosa*, and like it in possessing a truncate thumb (figs 90, 94, THM.), as well as an acuminate extension of the lower arm (L.A.) on Ford's sclerite (cf. fig. 22, *M. dryadosa*).

Further distinguishable from *M. dryadosa* as follows: (1) Subapical lobe (fig. 91, SUB.L.) not really lobate, its proximal (anterior) margin sloping gradually to mid-microspiculate area (M.MSP.) instead of markedly angling to form a distinct projection (fig. 20). (2) Transverse sclerotization (T.S.) of D.A.9 slightly arched proximad (concavely facing base of arm) instead of being sinuate, and with concave margin facing distally. (3) Ford's sclerite with dorsal margin of base of upper arm (figs 94, 97, U.A.) quite flat instead of convex (fig. 22). (4) Lower arm (L.A.) with a dorsal spur or tooth-like projection, instead of being rounded. (5) Fusion of lateral walls of aedeagal pouch (AE.P.-L.) with crochet process (CR.P.) well tanned, resulting quasi-crochet (Q.C.) well sclerotized throughout; the darker, crochet-like structure of Q.C. less than thrice as long (measured along dorsal margin, from caudal margin of phylax) as broad at middle in *M. thurmani*. In *M. dryadosa*, comparable tanned area of Q.C. much narrower, viz., 4 times as long as broad. (6) Caudal sinus of deltoid flap (DEL.FL.) much larger, e.g., almost equal in area to apex of hood (HD.) and median dorsal lobe (M.D.L.) above it, instead of being less than $\frac{1}{2}$ that size. (7) Caudal (subvertical) margin of ♂ sternum 8 (fig. 101, m3–t3) shorter; height to level of longer bristle at dorsocaudal angle (m3) subequal to length of bristle, not 25% greater than length of bristle (fig. 29), due to greater slope of dorsocaudal margin in *M. thurmani*. (8) Lumacaudate process (LUM.) narrowing from middle to apex, instead of being broadly subovate (fig. 12). (9) Female tergum 7 (fig. 99, 7 T.) with lobe below antepygidial base (L.L.7) with angle rounded off; not acute (fig. 26). (10) Anal stylet (fig. 89, S.A.) with a subapical ventral bristle. This missing in *M. dryadosa* (fig. 16). (11) Ventral lobe of caudal margin of ♀ 7 S. (figs 99, 102) almost as high as long, instead of apex about $\frac{1}{2}$ as high as long (fig. 27). (12) Subventral sinus of ♀ 7 S. with basal $\frac{1}{3}$ symmetrical, evenly curved instead of with dorsal margin sloping dorsocaudad almost immediately.

DESCRIPTIVE NOTES. Essentially otherwise like *M. dryadosa* (cf., fig. 86, head ♂ with fig. 4) except as follows. Dorsal margin of immovable process (fig. 92, P.) sinuate, but mainly convex. Mesal genitalic ridge of ♀ tergum 8 (fig. 102, M.R.8) resembling an inverted "Y" with rounded arms and a wide cleft. Spermatheca (figs 88, 102) with internal margin of bulga (B.) at base of hilla (H.) less oblique, about 35 40 . Perula of bursa copulatrix (P.B.C.) elongate-ovoid, nearly as long as broad in middle, more dilated ventrally than dorsally; anterior margin straight and subvertical; caudal margin somewhat convex. Sac (SAC.) of B.C. small, its volume scarcely exceeding that of P.B.C., the portion immediately dorsal to perula with height only equal to $\frac{1}{2}$ that of perula. Glandula vaginalis (G.VG.) feebly sclerotized; at times inapparent; sinuate. Paragenital morion (PG.M.) weakly tanned; indiscrete, presented as a narrow, ovoid structure lying across or near base of P.B.C. and perpendicular to it.

ILLUSTRATIONS

86. Head and prothorax (♂)
87. Movable finger
88. Spermatheca
89. Sensilium and anal segments (♀)
90. Apical region of aedeagus
91. Distal arm of sternum 9
92. Processes of clasper
94. Apex of aedeagus
97. Apical region of aedeagus
99. Sternum 7 (♀)
100. Lateral metanotal area (♂)
101. Sternum 8 (♂)
102. Spermatheca and genitalia

COMMENTS. The species is named for the late Deed C. Thurman in token acknoledgement of the many and significant contributions on the ecology, control and taxonomy of arthropod-vectors of disease in Thailand which Dr Thurman managed to make before his tragic death from cerebral malaria in that country at the height of his career.

M. thurmani is predominantly a flea of the ground-squirrel *Menetes berdmorei*, with occasional specimens occurring on *Tupaia*, as can be seen from the tabulation on page 245, which summarizes the data for paratypes. *M. thurmani* is evidently a widespread species in Thailand ranging, with its main host, over most of that country, and hence I suspect that it will be found on that ground-squirrel in northern Malaya and Indo-China.

8. **Medwayella calcarata** sp. nov.

TYPE MATERIAL. Holotype ♂ (B-49517) ex *Lariscus insignis*; WEST MALAYSIA: Perak, 8 mi W of Ipoh, Kledan Saiong Forest Reserve; elev. 1300 ft; 1.X.1958; Coll. R. Traub. Allotype ♀ (B-48637) ex *L. insignis*; Perak, Maxwell Hill; elev. 3000 ft; 25.VI.1958; Coll. R. Traub. Paratypes as follows: 3 ♂ with same data as holotype; 2 ♂ ibid. but elev. 1100 ft. 2 ♂ 10 mi NW of Ipoh; 29–30.VIII.1958; Coll. R. Traub. 1 ♂, 1 ♀ Perak, Maxwell Hill, Gunong Hijau; elev. 4200 ft; 21.III.1958; Coll. R. Traub.

Holotype (U.S.N.M. number 71606), allotype and 1 paratype deposited in U.S. National Museum. Paratype (1 ♂) in the British Museum and remainder in the author's collection.

DIAGNOSIS. Separable from all described species by virtue of the modified features of the head (fig. 104, ♂), viz.: (1) Labial palpus extending to apex of protrochanter instead of only to near tip of procoxa. (2) Distal segment of maxillary palpus also unusually long—1·75 times that of segment 3 instead of about 1·5 times. (3) With additional "supernumerary" bristles (SY.) on the preantennal region, e.g., 3 instead of 1 between rows II and III, with an extra 1 in row II, in ♂ making a total of 19 long or medium-sized bristles instead of the usual 16–17. Female with 1 "supernumerary," which is absent in most ♀ members of the genus.

Agrees with *M. loncha* (figs 118, 126–132) (and the 2 new species next described) in the following respects (and thereby differing from *M. dryadosa* and allies): (1) Re distal arm of ♂ sternum 9 (fig. 111): (a) Subapical lobe (SUB.L.) long and sharp-pointed, like a spur, instead of being lobate (figs. 20, 68). (b) Apical ½ of ventral (caudal) margin (qq–u3 in fig. 3; cf., also fig. 1) much more heavily sclerotized than anterior margin e3 qq). (c) Apex of ventral margin (g3-qq) appearing to project distad of arm as a rod-like extension (EXT.9) instead of curving to form an apical lobe (figs 20, 21, AP.L.). (d) With a caudal row of about 6 wide-set, fairly long, straight spiniforms instead of a subapical group (S.G.SPN.) of close-set, fairly small ones. (e) Tanned portion of dorsal margin distad of SUB.L. (c3–f3) extending only midway to apex, e.g., to distal end of supramedial flap (SUP.FL.) and then becoming semimembranous and curving toward ventral margin, thereby accounting for the apical rod-like extension. (2) Ford's sclerite of the grooved type (fig. 113, GRV.).

Readily separable from *M. loncha* as follows: (1) Movable finger (fig. 108, F.) not nearly as short and broad, viz., length distad from apex of immovable process (P.) (cf., fig. 1, n–s) 4 times breadth of F. at narrowest level (j–k), instead of scarcely more than thrice as long as broad there (fig. 126 ,F.). (2) Bases of setae of D.FR. forming a line tangential to main axis of F. (n–s) but almost subparallel to longitudinal axis of body of flea, instead of vice versa. (3) Sinus on apical (dorsal) margin of immovable process of clasper (P.) close to caudal margin and hence resulting in a dorsocaudal lobe, instead of bearing the sinus near the anterior margin and lacking a dorsocaudal lobe. (4) Manubrium with ventral margin lacking a distinct bulge (w) immediately anterior to sinus near posterior ⅓ (v) instead of being definitely convex there. (5) Distal arm of sternum 9 (fig. 111) relatively narrow at level of subapical lobe (SUB.L.) so that breadth (cf. fig. 3) (g3–d3) is only 1·3 times length of spur (d3–mm) instead of more than twice d3–mm (fig. 127). (6) Axis of EXT.9 (g3–qq) upcurved, directed more dorsad than caudad, instead of being straight, paralleling axis of D.A.9. (7) Tanned portion of quasi-crochet (fig. 113, Q.C.) about 1·7 times as long as broad, with dorsal margin slightly concave and nearly paralleling ventral one; anterior and posterior margins slightly convex. In contrast, in *M. loncha* (fig. 128) Q.C. only 1·3 times as long as broad; dorsal margin broadly convex; ventral margin angled at middle, with anterior ½ straight, horizontal, and posterior ½ concave, curving dorsocaudad; anterior and posterior margins straight, vertical. (8) Ford's sclerite with groove (GRV.) broad and with margins equidistant and essentially parallel throughout; not narrowed at area of contact with dorsal expanded apex of body of crochet (B.CR.) and again at dorsal apex of groove. (9) Upper arm (U.A.) of securifer lacking a sclerotized nubbin at apical (caudal) ⅓ where side of lower arm (L.A.) moves dorsad to link with U.A. (10) Distance between dorsocaudal angle of apex of B.CR. and nearby dorsocaudal angle of U.A. subequal to height of slightly concave or straight apical (caudal) margin of U.A. instead of being nearly double the height of arcuate apical margin of U.A. (11) Phylax much broader, viz., only slightly more than twice as long as broad at maximum girth (near ventral margin) instead of more than thrice. (12) Dorsal spur at apical ⅓ of sclerotized inner tube (S.I.T.) curved back over tube so that for most of its length it parallels S.I.T. and is close to it instead of being oblique to it. (13) S.I.T. broad proximad of dorsal spur but much narrowed distad (and ½ its diameter) instead of only being somewhat narrowed. (14) Angled base of subventral sinus on ♀ sternum 7 (fig. 103, 7 S.) quite diagnostic; in the other known female *Medwayella* from Malaya and Borneo the margin of the sinus is rounded (fig. 102). (15) Inner walls of sclerotized duct of bursa copulatrix (fig. 103, D.B.C.) in their entirety more tanned than bulk of perula, including anterior margin. In *M. loncha* only part of D.B.C. (fig. 118) well tanned, as is, at best, lower rear part of perula. (16) Dorsal anal lobe (fig. 103, D.A.L.) with 9 non-marginal bristles in 3 vertical rows preceding anal stylet, not with but 6 non-marginals in 2 irregular vertical rows (fig. 129). (17) Anterior margin of hilla (H.) of spermatheca protruding into bulga (B.) (internal margins) for ½ length of hilla, instead of ⅓ (fig. 132). (18) Anal stylet (A.S.) about 5·5 times as long as broad at middle, and there somewhat constricted, instead of 4·6 times and gradually narrowing from base towards apex and very slightly constricted subapically (fig. 129).

DESCRIPTIVE NOTES. The diagnosis above serves to cite differences from *M. dryadosa* as well (q.v.) but *M. calcarata* is otherwise quite similar, except as follows.

Male. About 19 large or medium preantennal bristles in 5 irregular rows (fig. 104). Squamulum horizontal. Sternum 8 with caudal margin straight except for rounded corners; almost entire (scarcely microdenticulate) near ventrocaudal corner; long bristle near dorsocaudal angle with 2 or 3 marginal or submarginal, medium bristles above it. Lumacaudate process (fig. 107, LUM.) with dorsal margin virtually horizontal and straight; ventral margin of lobate portion oblique and usually triconvex (trebly convex); apex broadly rounded; as measured from base of ventral margin, only about 1·1 times as long as broad at base, 1·6 times as long as broad at middle bulge and 2·5 times that of subapical bulge. Movable finger (fig. 108, F.) with caudal margin quite straight at level of apex of conical process (C.P.) (cf., fig. 1, q), which in turn is only about 4·5 times as long (e–h) as broad at middle (f–g). Distal arm of sternum 9 (fig. 111) about 8 times as long (ii–qq) as broad at level (jj) of transverse sclerotization (T.S.). Distance between bulge (cc) at upper ⅓ of anterior margin of proximal arm of sternum 9 and apex of arm (aa) subequal to that from bulge (cc) to height of convexity of posterior margin (ee). Sclerotized inner tube (fig. 113, S.I.T.) with ventral margin bearing only a very short and low bulge, hence most of margin straight and paralleling dorsal one to level of dorsal spur.

Female. Caudalmost large bristle on ventral lobe of sternum 7 (fig. 103, 7 S.) approximately equidistant from dorsal and ventral members of pair preceding it. Lobe at ventrocaudal angle of 8 T. relatively long and acute; about 2·3 times as long as broad at middle. Glandula vaginalis (G.VG.) long and narrow, single (not preceded by a companion-"gland"). Mesal genital ridge of tergum 8 (M.R.8) with anterior margin sinuate at point of branch of subhorizontal arm; portion beneath fork convex, so is that of upper members of fork. Anal stylet (A.S.) long and narrow; nearly 6 times as long as broad at apical ⅓; slightly constricted at middle; but margins essentially subparallel.

ILLUSTRATIONS

103.	Spermatheca, genitalia and anal segments	107.	Lumacaudate process
		108.	Processes of clasper

104.	Head and prothorax (♂)	111.	Distal arm of sternum 9
105.	Lateral metanotal area (♂)	113.	Apex of aedeagus

COMMENT. This species, known in Malaya from 11 specimens, was only found in two localities, both in Perak. Eight males were taken at the first area, viz., the limestone forest a few miles west of Ipoh at 1100–1300 ft elevation. The species was collected here only on 4 occasions, always from *Lariscus insignis*, and at times accompanied by *M. dryadosa*, which was more common on these ground-squirrels in the area than was *M. calcarata*. The second area was on Maxwell Hill, Gunong Hijau, 3000–4200 ft elevation, where 3 specimens (1 ♂, 2 ♀) were taken from 2 *Lariscus*. It seems likely that *Lariscus* will prove to be the most common host of this flea. The lack of records of *M. calcarata* in the well studied dipterocarp-forested hills near Kuala Lumpur is notable.

It is of interest that this species apparently occurs in Sarawak as well. Mr Lim Boo Liat collected 19 fleas from *Lariscus* 18 miles south of Kuching, of which 17 were males of the new species next described, 1 ♀ was *M. phangi tana* and 1 ♀ was inseparable from Malayan *calcarata* at the species level, including the long labial palpi and terminal maxillary palpal segment and the internal genitalia, etc.

The name *calcarata* is derived from the Latin term *calcar*, meaning a spur, and refers to the conspicuous spiniforms on the male sternum 9.

9. **Medwayella batibacula** sp. nov.

TYPE MATERIAL. Holotype ♂ (B-84199) ex *Lariscus insignis*; EAST MALAYSIA: Sarawak, Kuching, Bukit Stigang, Kampong Pangkalan Kuap; 27.XII.1968; Coll. Lim Boo Liat. Paratypes as follows: 11 ♂ with same data as holotype, but 26–28.XII.1968. 4 ♂ Sarawak, Tijirak, 19 mi S of Kuching; 7–12.I.1969; Coll. Lim Boo Liat. 1 ♂ Sarawak, Pueh; 7.VI.1958; Coll. T. C. Maa. Holotype (U.S.N.M. number 71607) and 1 paratype in U.S. National Museum. Paratypes in collections of Bishop Museum, British Museum (Natural History), the Canadian National Collection (Ottawa) and the author.

DIAGNOSIS. Near *M. calcarata* and agreeing with *M. loncha* in same respects as those cited in the previous description (number 8). Separable from *M. loncha* by at least diagnostic features numbers 1–3 and 5-9 cited for *M. calcarata*. Distinguishable from *M. calcarata* as follows: (1) Labial palpus not extending beyond apex of procoxa instead of reaching tip of trochanter. (2) Segment 4 of maxillary palpus only 1·6 times as long as third, not 1·75 times. (3) Inner dimensions of lateral metanotal area (fig. 106, L.M.) virtually as high as long instead of being definitely longer than high as in *M. calcarata* (fig. 105, L.M.) and *M. dryadosa* (fig. 5). (4) Third vinculum (V.C.3) with dorsal surface sinuate and strongly upcurved at apical $\frac{1}{2}$, the link-plate usually lying at an angle of about 45° except for distal curve into point of articulation in lateral metanotal area. In *M. calcarata*, V.C.3 is quite flat dorsally for about $\frac{1}{2}$ its length before curving towards L.M. and its axis is nearly horizontal, much as in *M. dryadosa*. (5) Margin of lobe at cephaloventral corner of mesepisternum virtually truncate instead of definitely sinuate as in the other 2 species (fig. 9, MPS.). (6) With a distinct bulge on ventral margin of manubrium (w in fig. 1, *q.v.* &

cf.) immediately anterior to sinus (v) near basal ⅓ instead of that region (w) being quite flat (even though sinus may be deep) as in *M. calcarata* and *M. dryadosa* (fig. 18, MB.). (7) Movable finger (fig. 109, F.) with caudal margin somewhat convex proximally, e.g., at point q, at level of apex of conical process (C.P.), instead of quite straight as in *M. calcarata* (fig. 108). (8) Dorsal margin of process of P. quite straight, lacking subapical sinus. (9) D.A.9 (fig. 112) with ventral (caudal) margin (*cf.* fig. 3, qq–u3) curving dorso-apicad at an angle of 45°, commencing just above point q3, somewhat distad of level of subapical lobe (SUB.L.), and resembling a flattened arc. Tip (qq) of apical extension (EXT.9) only slightly upturned. In *M. calcarata* (fig. 111) the dorso-apical curve commences more distad, at level of third spiniform from tip, and apex of EXT.9 is so upcurved that its tip (qq) is at right angles to longitudinal axis of arm. (10) Semimembranous portion of dorsal margin of D.A.9, above apex of supramedial flap (SUP.FL.) arcuate and joining EXT.9 at apex instead of being distally excised. (11) Sub-rhomboidal tanned portion of quasi-crochet (fig. 115, Q.C.) proportionately much longer and narrower, viz., more than twice as long as broad instead of 1·7 times. (12) Apicoventral corner of Q.C. produced into a short nubbin instead of being squared. (13) Body of crochet (B.CR.) much broader subdorsally, its breadth there subequal to maximum breadth of phylax (PHY.) instead of being only ⅓ that of PHY. (14) Securifer with groove (GRV.) broader at depth of curve than subapically (both dorsally and ventrally); breadth of groove never approaching that of base of upper arm (U.A.) instead of exceeding it throughout. (15) U.A. broad for most its length; length of basal ½ only equal to 2·5 times its breadth instead of more than 4 times. (16) Lower arm (L.A.) of securifer with apical margin angulate, not slightly concave. (17) Phylax (PHY.) proportionately narrower, viz., about 3·4 times as long as broad at maximum level (near base) instead of 2·3 times; its axis sinuate instead of straight for basal ⅔. (18) Sclerotized inner tube (S.I.T.) with dorsal spur arching dorsad but recurved towards axis of tube; its arc removed from S.I.T by a distance equal to 4–5 times breadth of base of spur. In *M. calcarata* the spur parallels tube for most its length and is close to it, the distance separating them less than twice basal diameter of spur. (19) S.I.T. subapically dilated instead of being of uniform diameter to apex.

(Female unknown)

DESCRIPTIVE NOTES. Differences from *M. dryadosa* are also included in the above diagnoses, and additional ones follow. Squamulum horizontal. Sternum 8 with cuadal margin slightly concave except for well rounded corners. Lumacaudate process (fig. 116, LUM.) neither well developed nor demarcated; lobate portion conical, with ventral margin commencing at level of 2 relatively long, stout ventromarginal bristles; length from here twice breadth at midline; with only about 16 close-set bristles, none of which truly spiniform, in 5–6 irregular rows. Movable finger (F.) with a mesal suture running from apex of stiva to middle of tip of F. (fig. 110 and approximating p–n in fig. 1); another mesal seam extending from base of distal fringe (D.FR.) transversely across F. to apical ⅓ of anterior margin. Distal arm of sternum 9 about 8 times as long (ii–qq) as broad at level (jj–uu) of transverse sclerotization (fig. 112, T.S.). Upper portion (bb–ff) of posterior margin of proximal arm of sternum 9 flat, subparallel to that of anterior margin (aa–dd).

ILLUSTRATIONS

106. Lateral metanotal area (♂)
109. Processes of clasper
110. Mesal aspect of F.
112. Distal arm of sternum 9
115. Apex of aedeagus
116. Lumacaudate process

COMMENT. All of the known specimens, 17 males representing 9 collections, were from *Lariscus insignis* in the same general area and habitat in Sarawak. (Usually female fleas are more common than males, at least in collections, and it is unprecedented to obtain such a large series of males in the absence of females.) The superficial similarity to *M. calcarata* from Perak in Malaya, and which might also be a *Lariscus* flea, is quite striking. The differences apparent on critical study, however, cited above, are too great for subspecies and indicate the two are sibling species. This belief is supported by the fact that a female virtually indistinguishable from Malayan *M. calcarata* was collected from the same host and locality as the type series of *M. batibacula* (along with a single female of *M. phangi*). It is highly unlikely that the length of the labial palp and all the other significant characters noted would vary only in the Sarawak male, while the female remained unchanged in the course of evolution. It seems most probable that *M. calcarata* occurs both in Sarawak and Malaya, parelleling the distribution of *M. phangi* and *M. robinsoni*. Further collections are urgently required to clarify this point and the many other questions posed by the chronic shortage of specimens of Siphonaptera for study from sundry hosts and habitats throughout most of the Asiatic-Pacific area.

The name *batibacula* is derived from the Latin words for thorn or spine (*batus*) and staff or rod (*baculus*), and the "thorny staff" refers to the distal arm of sternum 9.

10. **Medwayella veruta** sp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-19165-1) ex squirrel nest; EAST MALAYSIA; Sabah (N. Borneo), Mt. Kinabalu, Ranau; elev. 1500 ft; 31.VII.1953; Coll. R. Traub. Paratypes as follows: 5 ♂, 3 ♀ with same data as holotype. 2 ♂, 1 ♀ ex *Sundasciurus lowi*; loc. cit., but 13.VII, 6.IX.1953. 1 ♀ ex *Tupaia* sp.; loc. cit., but 2.VIII.1953. 1 ♂ ex *Ptilocercus lowi*; loc. cit., but 13.VII.1953; Coll. R. Traub & H. D. Newson. 2 ♂ ex *Tupaia* sp.; 18 mi S of Tenom Kg Bara Jumpa; 2.II.1963; Coll. J. A. Bullock.

Holotype (U.S.N.M. number 71608) and allotype in U.S. National Museum. Paratypes in British Museum (Natural History) (1 pair) and in author's Collection.

DIAGNOSIS. Agrees with *M. loncha* in the same respects as those listed for *M. calacrata* (*q.v.* number 8) and thereby instantly separable from *M. dryadosa* and allies, while the characteristic shape of D.A.9 of *M. veruta* (fig. 120), *M. batibacula*, etc., readily distinguishes this group from *M. phangi* (fig. 68) and its relatives.

Readily separable from *M. loncha* as follows: (1) Movable finger (fig. 119, F.) not nearly as foreshortened and broad subapically, viz., about 3·75 times as long (s–n in fig. 1, *q.v.* & *cf.*) as broad (j–k) below distal fringe (D.FR.); not merely thrice (fig. 126). (2) Bristles of D.FR. with bases forming an oblique line instead of a straight line paralleling longitudinal axis (s–n) of F. (3) F. with convexity of caudal margin (q) near P. exceeding that of cephalic margin (i) near conical process (C.P.) instead of being flatter than that of opposite margin. (4) Posterior margin of P. (t–u) somewhat convex below level of subapical long bristle instead of being straight to near sinus (v) near fulcral sclerite (F.S.). (5) Anterior (dorsal) margin of D.A.9 (fig. 120) with portion distad and proximad of spur (SUB.L.) (*cf.* fig. 3, e3–f3 & c3–kk) lying in different planes, D.A.9 being much broader proximad to SUB.L. than distad; instead of anterior margin forming a straight line (kk–qq) interrupted by spur. (6) Distance (e3–qq) from SUB.L. to apex of segment (EXT.9) shorter than in *M. loncha*, e.g., distance (b3–qq) from dorsal (anterior) apex of transverse sclerotization (T.S.) to tip of arm is 3·7 times distance (e3–qq) from upper margin of base of SUB.L. to apex of EXT.9, instead of only 2·7 times. (7) SUB.L. proportionately closer to upper limit of mid-microspiculate area (M.MSP.), viz., distance (c3–kk) between them subequal to length of bristles of caudomarginal submedian group (CM.G.B.) instead of clearly exceeding it. (8) Anterior margin of D.A.9 (e3–qq) extending to apex of arm even though lightly tanned distally, instead of curving caudad subapically (f3). (9) Deltoid flap of aedeagus (fig. 114, DEL.FL.) only twice as tall as long instead of 2·4 times. (10) Tanned portion of quasi-crochet (Q.C.) proportionately longer and narrower, thrice as long as broad at middle instead of 1·3 times. (11) Unique in that phylax (PHY.) is curved caudad apically so that there is a short, broad lobe at dorsocaudal corner. In other *Medwayella* the caudal margin is straight for the upper ½ and hence there is no lobe. (12) Phylax narrower than in *M. loncha* and more constricted subventrally, although both are broadest near middle. Length 3·2 times midgirth, and 4 times that at narrowest point, instead of 2·8 and 3·5 times. (13) Groove (GRV.) of Ford's sclerite widest at middle and narrowest near dorsal apex, instead of vice versa. (14) Upper arm (U.A.) of securifer with dorsal margin sinuate —the trough proximal and height of convexity just apicad of middle, whereas in *M. loncha*, dorsal margin is evenly concave to near apex. (15) Lower arm (L.A.) with upper margin convex or peaked near apex, not fairly straight (though microserrate). (16) Dorsal spur of sclerotized inner tube (S.I.T.) large, sloping cephalodorsad at angle of 60°, then recurved over tube and apex connected with it; resembling a triangle with a hollow center, whose base equals diameter of S.I.T. and whose altitude is about ⅔ that diameter. In *M. loncha* the spur commences more vertically, is apically recurved and presumably lacks elements returning anteriorly to S.I.T. (17) Subventral sinus of ♀ sternum 7 (figs 117, 124) open dorsally, there being no true notch, whereas in *M. loncha* (figs 118, 130) caudal margin above ventral lobe is inclined to an angle of about 60° until near apex of lobe, so that there is a notch. (18) Caudal margin of 7 S. (fig. 124) with a short but distinct median lobe where it recurves cephalodorsad. In *M. loncha* (fig. 130) curve is effected without production of a lobe. (19) Perula of bursa copulatrix (P.B.C.) relatively shorter and broader, viz., only about 2·2 times as long as broad at lower ⅓, instead of 4 times. (20) With a distinct "gland" between glandula vaginalis (G.VG.) and orifice of vagina; this lacking in *M. loncha*.

Descriptive notes. The characters cited above also differentiate *M. veruta* from *M. dryadosa* and additional points follow. Lateral metanotal area with quadrate untanned area taller than long. Squamulum horizontal and more than 5 times as long as broad at middle. Spiracular fossa of metepimere sagittate but with ventral margin straight and sloping somewhat dorsocaudad; dorsal margin slightly inclined from horizontal for first ½ and then sloping ventrocaudad towards apex; about 1·3 times as long as tall at maximum level. Spiracular fossa on 2 T. 1·6 times as long as broad; 2·3 times on 6 T. Lower antepygidial bristle about 2·5 times length of upper one in male; 2·4 times in female. With dorsal lower modified bristle (fig. 124, L.M.B.) a smaller, thinner version of upper antepygidial bristle; L.M.B.-2 resembling long bristles of adjacent row. Lower lobe of 7 T. (L.L.7) below A.B. blunt.

Male. Ventral extension of 8 SPC. with height subequal to or exceeding diameter of horizontal section. Lumacaudate process (LUM.) with densely bristled area about 2·4 times as long as high; apically broadly or obtusely rounded. Conical process (fig. 119, C.P.) about 5 times as long (e–h) as broad (f–g). Dorsocaudal corner of F. scarcely produced into a snout, e.g., stiva (STV.) poorly developed, in that distance (l–p) from anterior margin near apex (l) to tip of stiva (p) is 6·5 times length of stiva (p–o/k). Distal fringe (D.FR.) consisting of 4 or 5 bristles; lowermost the thinnest. Sinus of ventral margin of manubrium (v) long and shallow; the bulges (u and w) flanking it correspondingly short. Upper sinus (aa–cc) of anterior margin of P.A.9 much deeper than lower sinus (cc–dd), which is virtually flat. D.A.9 about 8 times as long (ii–qq) as tanned region is broad (uu–jj). With about 5 or 6 marginal spiniforms on caudal margin of D.A.9, of which lowest 4 are usually longest and stoutest, and distalmost of long ones generally at level of SUB.L. (d3–q3). Mid-microspiculate area (M.MSP.) highly convex and apically bulging above D.A.9 nearly as much as SUB.L., but cavity of receptacle with D.A.9 correspondingly fairly shallow. Lateral laminae of aedeagus and middle lamina relatively broadly yoked at tip of apex of apodeme, margins of the plates parallel until summit. Sinus of hood (HD.) deeply excised, reaching to near apex of B.CR. Upper margin of deltoid flap (DEL.FL.) evenly but shallowly concave. Vertical portion of phylax (PHY.) slightly sinuate.

Female. Spermatheca (fig. 123) with bulga (B.) bearing a short but distinct peak. Ventral lobe of sternum 7 short and broad; scarcely longer than tall. Anal stylet (fig. 122, A.S.) scarcely narrowed from base to near apex; about 4·6 times as long as broad at middle. Tergum 8 (fig. 125, 8 T.) broadly ovate at ventrocaudal angle, lacking a distinct lobe.

ILLUSTRATIONS

114.	Apex of aedeagus	122.	Anal lobes and stylet (♀)
117.	Spermatheca and genitalia	123.	Spermatheca
119.	Processes of clasper	124.	Sternum 7 (♀)
120.	Distal arm of sternum 9	125.	Genitalia (♀)
121.	Sternum 8 (♂)		

COMMENT. As can be seen from the type data, *M. veruta* was found on *Sundasciurus lowi*, on *Tupaia* sp., and in the nests of squirrels on the foothills at the base of Mt. Kinabalu. In addition, the author and H. D. Newson collected a male from a nest, occupied by a pen-tailed shrew (*Ptilocercus lowi*), in a branch in a tree in the same area. It is worthy of note that this species was also collected on *Tupaia tana* in Sarawak, in Division III at Nanga Balleh, near Kapit (R.T.). This constitutes only the second known instance of a North Bornean indigenous flea occurring in Sarawak (and apparently represents a distinct subspecies). (The other species is *Stivalius mjobergi* Jordan, 1926, described from Mt. Murud, which is just south of the border of N. Borneo.) However, the differences in the Siphonapteran fauna of Sarawak as compared to North Borneo, which superficially appear to be striking, may prove to be more apparent than real when the mountains of Sarawak are studied, and as more of the lower elevations in North Borneo are surveyed. This is discussed further below (Section A.14), and in the third article in the series.

The name *veruta* is a Latin term meaning armed with a spear or javelin and refers to the rod-like extension of the spined distal arm of sternum 9.

11. **Medwayella loncha** (Jordan, 1926) NEW COMBINATION

Stivalius lonchus Jordan, 1926. Novit. zool. 33:390, figs 11, 12; Costa Lima & Hathaway, 1946, Pulgas: 327; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 7(2):3.

To date this species has been known only from the single specimen collected by Dr E. Mjöberg ex *Tupaia* sp. in Sarawak, Mt. Poi, 5000 ft elev. described by Jordan in but 4 lines and illustrated by one figure showing the upper portions of the movable finger and distal arm of sternum 9. The published material is inadequate for recognition of the species, and in fact is misleading, for instead of the movable finger F. being "not essentially different," we now are aware of a sufficient number of species in the group to realize that F. *is* distinctive. The collection of *M. loncha* and the related new species, *M. batibacula*, by Lim Boo Liat in Sarawak, and the discovery of another allied new species, *calcarata*, plus access to the type specimen, have rendered clarification of the characteristics of *M. loncha* possible, as well as description of the hitherto unknown female.

Diagnosis. The salient features of *M. loncha* have been listed in the comparisons made above in the descriptions of the new species *M. calcarata* and *M. veruta*, *q.v.* It is readily recognizable in the ♂ by the relatively short, broad F. (fig. 126), which is scarcely more than thrice as long (from apex of immovable process P., *cf.* fig. 1, n–s) as broad at narrowest level (immediately below level of distal fringe, D.FR., or j–k). It is further characterized by a D.A.9 (fig. 127) bearing a distal, vertical "spur" (EXT.9) instead of being curved to form an apical lobe (*cf.* fig. 20, AP.L.) etc., and by an aedeagus (fig. 128) with a groove (GRV.) between alpha portion (ALPH.) and base of upper arm (U.A.) of securifer. The short, broad quasi-crochet (Q.C.) is diagnostic—region distad of phylax (PHY.) is only 1·3 times as long as broad because of markedly convex dorsal margin (but upper portion lightly tanned). Female distinguishable by the following combination of characters: (1) Sinus of sternum 7 (figs 118, 130, 7 S.) very broad apically, and already diverging markedly from ventral margin at base. (2) Perula of bursa copulatrix (P.B.C.) elongate-ovate, but with anterior margin quite straight. (3) Paragenital morion so lightly tanned as to be virtually inapparent. (4) Lacking a "gland" caudad to glandula vaginalis (G.VG.). (5) Mesal genitalic ridge of tergum 8 (M.R.8) with anterior margin sinuate; subhorizontal fork aborted; anterior branch of fork short and narrow. (6) Ventrocaudal corner of 8 T. with a short, broad lobe.

ILLUSTRATIONS

3.	Distal arm of sternum 9	129.	Sensilium and anal segments (♀)
118.	Spermatheca and genitalia	130.	Sternum 7 (♀)
126.	Processes of clasper	131.	Sternum 8 (♂)
127.	Distal arm of sternum 9	132.	Spermatheca
128.	Apex of aedeagus		

RECORDS. 2 ♂, 1 ♀ ex *Sundasciurus lowi;* EAST MALAYSIA: Sarawak, Tijirak, 19 mi S of Kuching; 28–30.XII.1968; Coll. Lim Boo Liat. 1 ♂, 1 ♀ ex *Tupaia tana*; loc. cit.; 26.XII.1968.

COMMENT. It seems significant that this species was collected only on *Sundasciurus* and *Tupaia* but not on *Lariscus* in the same area, and that the latter were parasitized by *M. batibacula*. The material herein described and figured as *M. loncha* agrees closely with the type specimen in the British Museum.

12. **Medwayella javana** (Jordan, 1933) NEW COMBINATION

Stivalius javanus Jordan, 1933, Novit. zool. 38:355–356, figs 76, 77; Costa Lima & Hathaway, 1946, Pulgas: 327; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 7(2): 3.

Another species known heretofore only from a single ♂ (and 3 ♀), *M. javana* was described from specimens collected from *Tupaia javanica occidentalis* (holotype ♂), "*Rattus bukit temmincki*" (probably *R. fulvescens temmincki*) (2 ♀), and *Callosciurus n. nigrovittatus* (1 ♀) at "Tjiboeni, Bandong, W. Java" (today known as Tjibuni, Bandung). The present descriptive notes and illustrations are based upon a pair collected from *Tupaia javanica* by J. M. Stusak of the B. P. Bishop Museum, 30.IX. 1965 at Tjibodas, Java, 5200 ft elev., and which agree quite closely with the original description and photographs of the type material.

DIAGNOSIS. Some cardinal characters have already been noted in the description of *M. arcuata, q.v.* Salient points are: (1) Distinctive amongst known *Medwayella* in that the movable finger (fig. 133, F.) is long and narrow, viz., portion distad of apex of immovable process P. (*cf.* fig. 1, r–n) is about 4 times as broad at level of apex of conical process (i–q) and 5 times as long as broad at middle of subapical constriction (j–k). (2) The only other species besides *M. arcuata* in which dorsal margin of distal arm of sternum 9 (fig. 124) is deeply arcuate subapically (ARC.) instead of either bearing a true notch (figs 20, 21) or being homolate (figs 68, 81). In *M. javana*, ARC. is fairly shallow, i.e., 5 times as long (*cf.* fig. 1, mm–pp) as deep at trough. (3) Apical lobe (AP.L.) extending more dorsad (cephalad) than subapical lobe (SUB.L.). (4) Aedeagus (figs 95, 96) of the *M. robinsoni* type in that thumb (THM.)is in the "cocked" position and lower arm (L.A.) of securifer is broad and apically blunt, not acuminate. (5) Height of THM. slightly less than breadth of apex. (6) Upper arm (U.A.) of securifer distally acute but broad to basal half. (7) L.A. with lower margin about 1·8 times as long (from edge of body of crochet, B.CR.) as broad at middle; dorsal margin angulate and sloping from middle towards ventrocaudal corner at angle of about 45°. (8) Tanned portion of quasi-crochet (Q.C.) fairly short and broad, about 2·6 times as long (from edge of phylax, PHY.) as broad at middle; subapically somewhat dilated and apex obtuse. (9) Sclerotized inner tube (S.I.T.) well upcurved beyond level of long, straight dorsal spur. (10) Lumacaudate process (fig. 135) well defined; narrow—with only 1 spiniform bristle at apex and no more than 3 or 4 per row in breadth; length (from anterior spiniform) about 1·75 times breadth at middle. (11) Sternum 7 of ♀ (fig. 40, 7 S.) unusual in that ventrocaudal lobe is sinuate apically. (12) Ventrocaudal sinus of 7 S. short, dilated apically. (13) Perula of bursa copulatrix (P.B.C.) pyriform, with expanded portion ventral, but anterior margin quite flat. (14) Paragenital morion (PG.M.) with a conspicuous tanned rod-like element buttressing P.B.C. (15) Mesal genital ridge of tergum 8 (M.R.8) with anterior and median margins sinuate; lower branch below fork short, thin and lightly tanned. (16) Caudoventral lobe of 8 T. fairly short, broad at base and with an angle of about 35° at tip. (17) With glandula vaginalis (G.VG.) long and thin; no other "glands" caudad of it.

Illustrations

40. Genitalia (♀)
95. Apex of aedeagus
96. Sclerotized inner tube
133. Processes of clasper
134. Distal arm of sternum 9
135. Lumacaudate process
136. Sternum 7 (♀)
137. Spermatheca, genitalia and anal segments

13. **Medwayella rhaeba** (Jordan, 1926) NEW COMBINATION

Stivalius rhaebus Jordan, 1926, Novit. zool. 33:389, figs 9, 10; Jordan & Rothschild, 1926, Sarawak Mus. Jour. 3 (part III) (10): 290, figs 6, 7; Costa Lima & Hathaway, 1946, Pulgas : 327; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 7(2) : 3.

This species is still known only from the single pair from "*Sciurus brooksi*" (*lapsus* for the squirrel now called *Sundasciurus brookei*) on Mt. Dulit (Sarawak) and from the abbreviated descriptions and figures by Jordan in 1926 and Jordan & Rothschild in 1926. The diagnostic features mentioned in the present article are based primarily upon photographs of the holotype (♂) and allotype in the British Museum.

Diagnosis. Apparently unlike any of the other described species in the shape of the movable finger (fig. 138, F.). At level of base of crochet process (CR.P.), breadth of F. exceeds that at apex, yet narrowed to half that breadth at apical third (measuring from base of CR.P. or summit of immovable process P.). F. rapidly broadening above that level, largely due to oblique caudal margin slanting at 45° to tip of stiva. Distal fringe (D.FR.) of 3 stout bristles inserted immediately below apex of stiva. Distal arm of sternum 9 (D.A.9) diagnostic by virtue of denticulate tip or nubbin at anterodorsal angle. Other characteristics are mentioned in comparisons made with *M. phangi* (number 5 above). The heavily sclerotized, arched, horizontal section of the mesal genitalic ridge of ♀ sternum 8 (fig. 139, M.R.8) seems to be unique amongst known *Medwayella*.

M. rhaeba agrees with *M. phangi* in being a species with a grooved Ford's sclerite (GRV.), with a narrow, upturned quasi-crochet (Q.C.) and with a homolate D.A.9 (*cf.* figs 68, 71, *M. phangi*). However, the differences are striking, as has been pointed out above.

ILLUSTRATIONS

138. Modified abdominal segments (♂)
139. Modified abdominal segments (♀)

14. GEOGRAPHIC AND HOST-DISTRIBUTION OF **MEDWAYELLA** IN MALAYA

A consideration of the ecological, geographic and host-distribution of *Medwayella* is worthwhile even though virtually nothing is known about the flea-fauna of the eastern districts of the Indian subcontinent (such as Assam, Manipur, the Chittagong Hills, etc.) and of the bulk of the Indonesian Archipelago (i.e., except Sumatra and Java, for which we have sparse information) and despite the fact that data are minimal for the northern and eastern parts of the Indo-China subregion.[6] Thus, even though collections from the peripheral regions of the range for *Medwayella* are sorely needed, it is possible to make some generalizations which seem significant. The zoogeographical observations and implications in the main are discussed in the third article in the series, and what follows here will largely deal with the types of hosts infested and where they were found.

Thirteen species of *Medwayella* are mentioned in this paper. Six of these are known from Sarawak, five from Malaya, two from Sumatra, two from Thailand and one each from Sabah (N. Borneo), Java and Indo-China. Of the 13, *M. robinsoni* is known from four of the areas listed (Malaya, Java, Sarawak and Thailand), and two species (*M. calcarata* and *M. phangi*) occur in both Sarawak and Malaya. (The fact that some are found in several countries, of course, meant that the numbers just cited will add up to more than 13.) This recorded distribution, to a great extent, reflects the degree of collecting done per area, but even so, certain trends suggested by the data are valid. Thus, while as yet undescribed species undoubtedly exist in Indonesia, and two such are known from the Philippines, and the genus probably occurs in eastern India and Burma, sufficient field-work has been done in Indo-China and Thailand to show that the number of endemic species of *Medwayella* is well below that for Malaya and Borneo, which seem to be the center of development of the genus.

Of the countries mentioned, the only one for which there are sufficient data for detailed discussion of hosts and distribution in Malaya, and the available records are summarized in Tables 1 to 6. (It is reiterated that the numbers of hosts cited in Table 2 as having been examined includes only our own collections, and thus these do not represent the hosts trapped or shot by our colleagues in Kuala Lumpur. The numbers of fleas, however, do include all available specimens.)

The sciurids listed as tree-squirrels (T) in Table 2 are essentially arboreal and nest high in the trees, but do come to the ground on occasion. The ground-squirrels and ground-dwelling forest-rats (marked G) spend most of their time on the forest-floor

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[6] It should be noted that the geographic names and expressions used in this article are those that have a fairly specific connotation in zoogeography, history or usage. Thus, there are no political considerations in the term "Indo-China," which is an established name for a zoogeographical subregion. Similarly, to a naturalist, "Malaysian" includes lower Burma and some of the Indonesian Islands, and hence this term has been avoided when speaking of the country formerly called Malaya, or of the part of Borneo previously under British rule. The expression "Malayan" as used here, refers to the Peninsula and does not have the zoogeographic connotation of a Malayan (or Malaysian) subregion.

TABLE 2

HOST-DISTRIBUTION OF FIVE *MEDWAYELLA* FLEAS ON THE MALAYAN PENINSULA

Hosts			Fleas—Numbers and percentages of *Medwayella* species										
		Minimum Number	*dryadosa*		*phangi*		*limi*		*calcarata*		*robinsoni*		
Name	Habits	Exam'd	No.	%	No.	%	No.	%	No.	%	No.	%	Totals
1. *Callosciurus caniceps*	T	184	–	–	–	–	1	3%	–	–	92	9%	93
2. *Callosciurus erythraeus*	T	38	–	–	–	–	–	–	–	–	6	•	6
3. *Callosciurus nigrovittatus*	T	110	–	–	–	–	–	–	–	–	139	14%	139
4. *Callosciurus notatus*	T	259	–	–	2	3%	–	–	–	–	206	20%	208
5. *Callosciurus prevosti*	T	18	–	–	–	–	–	–	–	–	4	•	4
6. *Sundasciurus hippurus*	T	23	–	–	–	–	–	–	–	–	28	3%	28
7. (Arboreal Squirrel Nest)	(T)	6	–	–	–	–	–	–	–	–	32	3%	32
8. *Sundasciurus tenuis & S. lowi*	T + G	348	1	•	27	39%	–	–	–	–	212	21%	240
9. *Tamiops macclellandi*	T + G	45	1	•	–	–	–	–	–	–	4	•	5
10. *Tupaia glis*	T + G	211	12	9%	33	49%	1	3%	–	–	193	19%	239
11. *Tupaia minor*	T + G	36	–	–	1	1·5%	–	–	–	–	9	•	10
12. Forest Rats (Scansorial)	T + G	117	–	–	–	–	1	3%	–	–	32	3%	33
13. Forest Rats (Ground)	G	362	7	5%	1	1·5%	–	–	–	–	11	1%	19
14. *Dremomys rufigenis*	G	74	3	2%	–	–	–	–	–	–	6	•	9
15. *Lariscus insignis*	G	52	20	15%	4	6%	3	7%	11	100%	9	•	47
16. *Rhinosciurus laticaudatus*	G	23	85	65%	–	–	36	84%	–	–	12	1%	133
17. (Other)	–	102	1	•	–	–	–	–	–	–	15	1%	16
Totals			130	±100%	69	100%	42	100%	11	100%	1010	±100%	1261

T = Tree-dwelling G = Ground-dwelling • = less than 1%

and nest below the surface, as amongst the roots of trees, but at times climb on tree-trunks and low trees and shrubs. *Tupaia* are active on the ground and are also at home on trees, at least on lower limbs. Their common name, tree-shrew, therefore is at least partially correct (since most mammalogists no longer regard them as shrews). The *Tupaia* and the scansorial forest-rats and the squirrels like *Sundasciurus tenuis*, *S. lowi* and *Tamiops maclellandi*, which can be seen and/or collected both on trees and the forest-floor, are designated as "T + G," for "tree and ground." Flying-squirrels, e.g., *Petaurista* and the giant tree-squirrel, *Ratufa*, were collected too seldom for discussion, but no characteristic species of fleas have been found on the 15–20 specimens of each examined by me in Malaya, while "strays" like *M. robinsoni* were rare. (It is interesting that in the Himalayas, *Petaurista* and *Hylopetes* flying-squirrels are infested with several fairly specific genera and species of fleas of Indo-Malaysian affinity and that in Formosa *Petaurista* regularly bears fleas, but of a palearctic species. An endemic genus has also been found on *Hylopetes* in N. Borneo.)

Several points are readily apparent from the data in Table 2. For example, of the five species listed, only *M. robinsoni* has been taken with any frequency on *CalloscPLACEHOLDER*

TABLE 3

HOST-DISTRIBUTION OF FIVE SPECIES OF *MEDWAYELLA* FLEAS ON THE MALAYAN PENINSULA (SUMMARY)

HOST	SPECIES OF MEDWAYELLA				
	DRYADOSA	PHANGI	LIMI	CALCARATA	ROBINSONI
I. ARBOREAL SQUIRRELS		3%	2%		49%
II. SEMI-ARBOREAL AND GROUND-SQUIRRELS	85%	46%	93%	100%	25%
III. TUPAIA	10%	50%	2%		21%
IV. FOREST-RATS	5%	1%	2%		4%
TOTAL %	100%	100%	±100%	100%	±100%
TOTAL NUMBER OF FLEAS	129	68	42	11	963

rus, a genus of tree-squirrels. In fact, of the remaining four species, only *M. phangi* and *M. limi* were ever collected on an arboreal squirrel and then only once each, i.e., two of the former from *C. notatus* and one from *C. caniceps* for the latter. In contrast, 65% of the records for *M. dryadosa* and 84% of those for *M. limi* were from *Rhinosciurus laticaudatus*, a ground-squirrel. Nearly half of the *M. p. phangi* were collected on the tree-shrew, *Tupaia glis*, but 39% were from the small *Sundasciurus* squirrels, which are frequently on the forest-floor. The second most prevalent host for *M. dryadosa* was the ground-squirrel, *Lariscus insignis*, accounting for 15% of those collected. All of the known Malayan *M. calcarata* likewise were from that host. However, the numbers involved (11 specimens) are too low for certainty regarding host-specificity of *M. calcarata*, although they represent seven different collections.

The apparent dearth of *Medwayella* reported from the ground-squirrel *Dremomys* seems noteworthy, but is misleading in a sense, since this squirrel is montane and the *Medwayella* being discussed are rare or absent above 4000–5000 ft. The host-range of *M. robinsoni* is obviously far greater than for other members of the genus, e.g., it was collected at least once on each type of host. The highest percentages, however, are for the arboreal and the partially arboreal squirrels, rats and tree-shrews.

These data are summarized in Table 3 below, which compares the numbers and percentages of these fleas which were from arboreal squirrels with those from squirrels that divide their time between trees and the ground, and with those from *Tupaia* and rats. From this table, it can be seen that 100% of *M. dryadosa* were from non-arboreal species (accounting for the name of "hater of tree-dwellers"), and that this same tendency was exhibited for *M. p. phangi* and *M. limi* (97% and 98% from ground-dwelling or semi-arboreal hosts respectively). The tree-shrews, *Tupaia*, were "good" hosts for at least three of the five species, particularly *M. phangi* and *M. robinsoni*. Various species of forest-rats, such as the scansorial *Rattus* (*Lenothrix*) *canus* and *R.* (*Maxomys*) *cremoriventer* and the ground-dwelling *R.* (*Lenothrix*) *rajah*, *R.* (*Leopoldamys*) *sabanus* and *R.* (*Stenomys*) *bowersi* at times carried one or two *Medwayella* fleas, generally *M. robinsoni*, but occasionally *M. dryadosa*, and rarely one of the others.

When discussing host-relationships, it is always important to consider infestation-rates. Unfortunately, the data here have limitations, even though for our own collections we have records of the numbers of animals which had no fleas at the time of examination. As mentioned above, since the collections were made to obtain living mammals for studies on scrub typhus, etc., many of the rats had been in the traps for hours, or even more than a day, before being placed in a bag for subsequent examination. Such excited hosts, perhaps drenched by rain, soon lose their fleas, while the ubiquitous and innumerable ants promptly ruin mammals killed by other types of traps. Under such condition, it is impossible to obtain reliable "flea-indices" or infestation-rates, and it is not surprising that the average number of *Medwayella* fleas per mammal in the tables above at times would be less than one, even if the "minimum number examined" were the actual total number. However, it is important to note that nearly all of the tree-squirrels and many of the *Tupaia* and ground-squirrels had been collected by shooting and the specimens were then immediately bagged. Even so, the over-all index was frequently below one flea per host, though an occasional squirrel would have as many as six or even ten *Medwayella*. No pattern could be determined for the marked variations in numbers noted for squirrels shot in the same locality and on the same day, although I suspect that factors such as sex (lactating females versus males, for example), age, season, etc., all play a role. More data are required in this regard.

Some idea of the infestation-rate can be obtained from the "collection rate" or the number of times the particular fleas were collected from a specific type of host (e.g., the numbers of hosts "positive" for that species of flea). These data are shown, where significant or relevant, for the four new species of *Medwayella* and for *M. robinsoni* (Table 4). These figures also are valuable because they offset the skewing effect of a single unusually large collection, which, while unrepresentative, may exert considerable influence on the mean or total number reported.

TABLE 4

THE NUMBERS OF SPECIMENS OF CERTAIN SPECIES OF *MEDWAYELLA* AND THE NUMBER OF TIMES THESE SPECIES WERE COLLECTED FROM SPECIFIC HOSTS IN MALAYA

	Species of *Medwayella*									
Host	*dryadosa*		*phangi*		*limi*		*calcarata*		*robinsoni*	
	Fleas	Coll'ns	Fleas	Coll'ns	Fleas	Coll'ns	Fleas	Coll'ns	Fleas	Coll'ns
Sundasciurus tenuis & S. lowi	1	1	27	13	–	–	–	–	212	113
Lariscus insignis	20	16	4	4	3	3	11	7	9	6
Rhinosciurus laticaudatus	85	26	–	–	36	15	–	–	12	9
Tupaia glis	12	8	33	18	1	1	–	–	193	82

The data suggest that the indicated association between *M. phangi* and *Sundasciurus tenuis* and *S. lowi* is a fairly close one, since this species was collected from those squirrels on 13 different occasions, even though the total number (27) is small. The same seems true for *M. robinsoni* on these hosts. *M. dryadosa* was relatively frequently taken on *L. insignis* and *Tupaia*, but in small numbers, whereas in the case of *Rhinosciurus*, the average infestation rate was over three (26 collections totalling 85 fleas). The facts that *M. calcarata* was collected from *Lariscus* on seven different occasions (with a total of 11 fleas) and was never taken on another host, suggest an intimate relationship, but additional data are required for verification of this point.

Thus far we have been dealing with *Medwayella* fleas and reported collections from sundry hosts. It is also worthwhile to consider the data from the converse view, viz., the major hosts and the relative numbers of *Medwayella* with which each kind was infested. This is shown in Table 5, whence it can be seen that virtually all the fleas taken on each of the three species of *Callosciurus* were *M. robinsoni*, and that 80% or more of the fleas from *Tupaia* and forest rats belonged to this species. *Lariscus* was most apt to be infested with *M. dryadosa*, although all five species were found on this host at one time or another. Of the 133 fleas reported for *Rhinosciurus*, 64% were *M. dryadosa* and 27% *M. limi*. The absence of *M. phangi* on this host is quite striking, particularly in view of the fact (mentioned below) that *M. phangi* was collected in areas where this ground-squirrel occurred.

TABLE 5

THE MAIN HOSTS OF *MEDWAYELLA* FLEAS IN MALAYA AND THE RELATIVE PERCENTAGES PER SPECIES WITH WHICH THEY WERE INFESTED

SPECIES OF MEDWAYELLA	CALLOSCIURUS			TUPAIA GLIS	FOREST RATS	LARISCUS INSIGNIS	RHINO-SCIURUS LATI-CAUDATUS
	CANICEPS	NIGRO-VITTATUS	NOTATUS				
DRYADOSA				5%	13%	43%	64%
PHANGI			1%	14%	2%	9%	
LIMI	1%			●	2%	6%	27%
CALCARATA						23%	
ROBINSONI	99%	100%	99%	80%	83%	19%	9%
TOTAL %	100%	100%	100%	100%	100%	100%	100%
TOTAL NO. OF FLEAS	93	140	208	239	52	47	133

● = less than 1%

The major collecting-localities in Malaya are shown in Table 6, while comments on the habitats in the area have been presented above (p. 207). It is apparent at a glance that *M. robinsoni* was found in all of the regions surveyed, and common in those wherein sufficient material had been collected. In all probability, this species will prove to be abundant in the little-studied Kelantan area and all other *inland* habitats below 4500 ft elevation where *Callosciurus* occurs.

As previously mentioned, we have never collected indigenous fleas along the coastal areas of Malaya (nor along the coast of any other humid tropical country), despite fairly intensive search in some regions, and the presence of species of hosts like *C. caniceps*, *Tupaia*, *R. sabanus*, etc., which carry fleas when farther inland. Indigenous fleas have not been collected on the Sembilan Islands, Pangkor Island and the Langkawi Islands. However, the rodent fauna varies on those islands—only rats occur on the first-named, and rats and tree-shrews are present on Pangkor, while on Langkawi *C. caniceps* was the only squirrel noted, but tree-shrews and sundry forest-rats were found to be plentiful. It is my belief that it is too warm and humid for fleas (or,

TABLE 6

RELATIVE ABUNDANCE OF SPECIES OF *MEDWAYELLA* IN MAJOR COLLECTING-AREAS IN MALAYAN PENINSULA

Species of **Medwayella**	1. Kuala Lumpur Forest	2. Subang Forest	3. Ipoh Hills	4. Gunong Benom	5. E. Coast Forest	6. Kelantan Forest	7. Mountains	8. Kedah
dryadosa	**	*	*	**	⊕	⊕	*	*
phangi	R	**	**	–	–	–	@	**
limi	**	–	–	–	**	–	–	–
calcarata	–	–	*	–	–	–	–	–
robinsoni	***	**	**	**	**	*	*	**

*** = Prevalent ** = Fairly Common * = Occasionally Collected
⊕ = Present, but data inadequate R = Rarely Taken @ = Collected on Kedah Peak

probably, their larvae) in such habitats, but the apparent absence of fleas on Langkawi at 2000 ft elevation is somewhat surprising, and further investigations are desirable to obtain better data in this regard, since we only examined a few rats taken at that height. The fact that *M. robinsoni* and *M. dryadosa* occur on Tioman Island off the east coast, is probably due to the presence of a monsoon season there, which may create favorable conditions for fleas in the dry spell. If so, then *M. robinsoni* may also prove to be present in the northeast coastal region of Malaya, where the climate is also somewhat different from that associated with the typical rainforests of that country.

As for the altitudinal range of *M. robinsoni*, it has been mentioned above that we have a few records of this species occurring (on *C. caniceps*) as high as 5000 ft, at the edge of montane forest, but their presence at such climes seems to be exceptional. Other species of fleas, especially the genus *Macrostylophora* Ewing, 1929, seem to be more characteristic of the higher altitudes, where *Callosciurus erythraeus* is the most abundant tree-squirrel and *Dremomys* the prevalent ground-squirrel. At the other extreme, *M. robinsoni* has been found on squirrels in inland forest only 50 ft above sea-level.

M. dryadosa is another species that was also taken in all of the localities listed in Table 6, although it never was collected as frequently as *M. robinsoni*, probably because its main host, viz., ground-squirrels like *Rhinosciurus* and *Lariscus*, are more difficult to trap or shoot than are *Tupaia* and *Callosciurus*. It seems to be most prevalent in relatively undisturbed dipterocarp forest in the foothills, as at Ulu Gombak, Ulu Langat, etc., in Selangor and at Gunong Benom, rather than in the limestone hills of Perak, the montane forest, or in the lowland, highly modified forest of Subang.

The distribution of *M. phangi* is quite different, although it too ranges widely over Malaya. It was rarely noted in the dipterocarp forest in the foothills of Selangor, and then only at the extreme edges, which has been secondary forest for several decades. In contrast, it was quite common in the highly disturbed forest at Subang (400–700 ft elev.), in the limestone hills of Perak (150–250 ft elev.), at Kedah Peak and at Bukit Wang Forest Reserve in Kedah. The occurrence of *M. phangi* on

Kedah Peak, in contrast to the other mountains studied, is of interest and is commented on below. The fact that 50 % of the specimens came from *Tupaia* and 39 % from *Sundasciurus tenuis* and *S. lowi* is in accord with this belief that *M. phangi* is associated with secondary forest. The absence of records of *M. phangi* from *Rhinosciurus* is noteworthy, and suggests that this ground-squirrel is primarily a denizen of undisturbed forest, an impression that is heightened by the numbers of collections of *M. limi* and *M. dryadosa* from this host. In this regard it is worth noting that the only area besides the dipterocarp forest near Kuala Lumpur where *M. limi* was found was in the forests of Trengganu, at Bukit Besi, near the east coast.

Although the zoogeography of *Medwayella* and other fleas will be discussed in the third paper in this series, attention is now called to the odd distributional pattern exhibited by some species of *Medwayella*. Three of the species, *M. phangi*, *M. calcarata* and *M. robinsoni*, are known from both Malaya and Borneo, but, in each case, only from Sarawak, not North Borneo (Sabah). Further, two of these have been found only in the western part of Malaya and are common in the Perak-Kedah regions.

15. KEY TO THE KNOWN SPECIES AND SUBSPECIES OF **MEDWAYELLA**[7]

1 Labial palpus long, extending to apex of fore-trochanter (fig. 104). Distal segment of maxillary palpus unusually long, 1·75 times length of third segment. ♂ with 3 "supernumerary" bristles (SY.) between rows II and III on head; ♀ with 1 such **calcarata** sp. nov. (p. 247)

– Labial palpus shorter, extending generally only to or near apex of procoxa (fig. 4), rarely to middle of fore-trochanter. Distal segments of maxillary palpus only 1·5 times length of third segment. ♂ with 1 supernumerary bristle (SY. and fig. 2); ♀ generally with none 2

2 Males 3

– Females[8] 18

3 Distal arm of sternum 9 (figs 20, 21, D.A.9) with a distinct subapical notch (NCH.) on anterior (dorsal) margin 4

– D.A.9 lacking distinct subapical notch; instead, anterior margin flat between apex and subapical lobe (figs 67, 112, SUB.L.) or else arcuate (fig. 33, ARC.) . . . 9

4 Ford's sclerite of aedeagus with a thumb-like process (figs 42, 44, THM.) on alpha-portion (ALPH.) which extends well above base of upper arm (U.A.) of securifer. Upright portion of ALPH. much broader for ventral ⅔ than subapically . . . 5

– Ford's sclerite lacking thumb-like process of alpha-portion (fig. 45, ALPH.); apex of ALPH. in line with base of upper arm (U.A.) of securifer. Upright portion of ALPH. rod-like . . . . **angustata** sp. nov (p. 227)

5 Margins of apical lobe of D.A.9 (fig. 20, AP.L.) truncate. Thumb (figs 22, 42, THM.) about thrice as long (tall) as broad . . . . . **dryadosa** sp. nov. (p. 215)

– Margin of apical lobe of sternum 9 (figs 53–55, AP.L.) angled or with upper half convex. Thumb (figs 56–58, THM.) only 1·2 times (or less) as tall as broad **robinsoni** subspp. 6

6 Upper ½ of margin of apical lobe (figs 21, 55, AP.L.) of D.A.9 distinctly convex. Notch (NCH.) with lower margin 1·5–2 times as long as upper margin . . . 7

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[7] Only one of the alternates cited need apply; these are not combined characters.

[8] The females of *M. rhaeba* (Jordan, 1926) and *M. batibacula* sp. nov. are unknown.

– Upper ½ of margin of apical lobe (figs 53 54, AP.L.) of D.A.9 quite straight or only slightly convex. Notch (NCH.) with lower margin only slgihtly longer than upper margin 8

7 Lower ½ of apical lobe (fig. 21, AP.L.) concave. Lower arm of securifer (figs 23, 44, L.A.) with apex not relatively acuminate; its caudal margin quite straight to near apex. Tanned portion of quasi-crochet (Q.C.) about 4 times as long as broad at middle. (Malayan peninsula) . . ***robinsoni robinsoni*** (Roths., 1905) (p. 233)

– Lower ½ of apical lobe (fig. 55, AP.L.) almost straight. Lower arm of securifer (fig. 57, L.A.) with apex somewhat acuminate due to subventral curve of caudal margin. Tanned portion of quasi-crochet (Q.C.) 3·5 times as long as broad at middle. (Sarawak) . . . . . ***robinsoni peregrinata*** subsp. nov. (p. 234)

8 Upper arm of securifer (fig. 58, U.A.) with apical snout relatively broad, about 2·5 times as long (from vertical internal root) as broad at middle; diameter at middle nearly as broad as subapical portion of lumen of sclerotized inner tube (S.I.T.). Margin of apical lobe (fig. 54, AP.L.) of D.A.9 quite flat and evenly angled at middle. (Java) . . . . ***robinsoni bogora*** subsp. nov. (p. 235)

– Upper arm of securifer (fig. 56, U.A.) with snout comparatively narrow, about 3–4 times as long as broad near middle; its diameter at middle much narrower than subapical lumen of S.I.T. Apical lobe (fig. 53, AP.L.) of D.A.9 with lower ½ of margin slightly concave; the angle at middle blunt. (Tioman Island, Malaya) ***robinsoni tiomanica*** subsp. nov. (p. 236)

9 Ford's sclerite of aedeagus with a distinct groove (figs 71, 113, GRV.) between alpha-portion (ALPH.) and securifer; but lacking a thumb-like apex to ALPH. Anterior margin of D.A.9 flat immediately above base of subapical lobe (figs 67–68, 111-112, SUB.L.) 10

– Ford's sclerite lacking a distinct groove (figs 94–95, 97–98); thumb (THM.) well developed instead. Anterior margin of D.A.9 arcuate (figs 33, 91, 134, ARC.) above base of subapical lobe (SUB.L.), the arc extending for at least ⅓ length of margin above SUB.L. 16

10 Movable finger (fig. 138, F.) with breadth of subapical constricted area less than ½ that of very broad base and equally broad apex. D.A.9 with a delimited nubbin at anterodorsal angle . . . . ***rhaeba*** (Jordan, 1926) (p. 257)

Movable finger (figs 67, 109, 119, F.) with constricted area not as narrowed; always much broader than ½ breadth of apex and generally so for base. Lacking a distinct nubbin at anterodorsal angle of D.A.9, although apex may be pointed (figs 67, 111, 127) 11

11 Caudal margin of D.A.9 heavily sclerotized and apically appearing as a rod-like extension (figs 112, 120, EXT.9); opposite margin lightly tanned. Spiniforms of D.A.9 relatively long and narrow, well spaced. Subapical lobe (SUB.L.) of D.A.9 spur-like. Distal ⅓ of quasi-crochet not appreciably narrower than basal part (figs 114, 128, Q.C.) 12

– Caudal margin of D.A.9 curving subapically (figs 67, 81) and hence not rod-like; not heavily sclerotized; anterior margin tanned to apex. Spiniforms of D.A.9 short and at times close-set. Subapical lobe (SUB.L.) broadly triangular and apex blunt. Distal ⅓ of quasi-crochet much narrower than basal portion, appearing like a tongue-like extension (figs 71, 82, Q.C.) 14

12 Movable finger (fig. 126, F.) short and broad, scarcely more than thrice as long (above apex of immovable process, P.) as broad at narrowest level (immediately below distal fringe (D.FR.)). Relatively tanned portion of quasi-crochet (fig. 128, Q.C.) short and broad, only 1·3 times as long as broad because of markedly convex dorsal margin . . . . ***loncha*** (Jordan, 1926) (p. 255)

– Movable finger (figs 109, 119, F.) at least 3·75 times as long as broad at narrowest level. Tanned portion of quasi-crochet (figs 114, 115, Q.C.) at least twice as long as broad 13

13 Movable finger (fig. 109, F.) relatively broad throughout, about 3·75 times as long as broad below distal fringe (D.FR.). Tanned portion of quasi-crochet (fig. 115, Q.C.) nearly straight, not angled upwards (but slightly curved)
batibacula sp. nov. (p. 250)

– Movable finger (fig. 119, F.) much broader basally than at constricted area below D.FR.; about 5 times as long as broad at constriction. Quasi-crochet (fig. 114, Q.C.) angled at middle so that distal ½ is at an angle of about 40° with proximal
veruta sp. nov. (p. 252)

14 Movable finger (figs 65, 66, F.) with caudal margin somewhat excised immediately below distal fringe (D.FR.) so that apical portion of F. appears almost stalked. Bases of D.FR. forming a line that is almost perpendicular. Groove of Ford's sclerite extending dorsad together, of equal length (fig. 71, GRV.)
phangi sp. nov. & subsp. nov. 15

– Movable finger (fig. 80, F.) with caudal margin evenly and slightly concave below distal fringe (D.FR.); apical portion of F. not differentiated. Bases of D.FR. forming a markedly oblique line. Groove of Ford's sclerite (fig. 82, GRV.) incomplete dorsally, margin of alpha-portion (ALPH.) extending more distad (dorsad) than opposite member and then forming a characteristic, broad truncate flap . . . . ***limi*** sp. nov. (p. 242)

15 Movable finger (fig. 65, F.) relatively narrow and arched, so that distal fringe (D.FR.) is on a short stalk. Breadth of F. at constriction much shorter than distance between proximal-most bristle of D.FR. and apex of F. Tip of subapical lobe of D.A.9 (fig. 67, SUB.L.) much closer to dorsal margin of median microspiculose area (M.MSP.) than to apex of D.A.9. (Sarawak) ***phangi tana*** subsp. nov. (p. 242)

– Movable finger (fig. 66, F.) with distal fringe (D.FR.) not on a short stalk. Breadth of F. at constriction subequal to distance between basal bristle of D.FR. and apex of F. Tip of SUB.L. further removed from apex of median microspiculose area (M.MSP.), distance only slightly less than that between SUB.L. and apex of D.A.9
phangi phangi sp. nov. (p. 240)

16 Movable finger long and evenly narrow (fig. 133, F.) about 5 times as long (distad of apex of immovable process, P.) as broad immediately below distal fringe (D.FR.); caudal margin straight near base so that F. is 4 times as long as broad at level of apex of conical process (C.P.). Quasi-crochet with sclerotized portion (fig. 95, Q.C.) relatively short and broad, about 2·6 times as long as broad at middle
javana (Jordan, 1933) (p. 256)

– Movable finger (figs. 34, 92, F.) much broader in proportion and caudal margin markedly bulging near level of conical process (C.P.); at most, scarcely more than 4 times as long as broad below distal fringe (D.FR.) and 2·4 times as long as broad at level of apex of C.P. Tanned, dark portion of Q.C. long and narrow, at least thrice as long as broad at middle (figs 97, 98) 17

17 D.A.9 (fig. 33) with a deep, symmetrical arcuate sinus (ARC.) extending from tip of subapical lobe (SUB.L.) to apex of apical lobe (AP.L.). Ford's sclerite with thumb (fig. 98, THM.) short in height, broader than high. Lower arm (L.A.) of securifer terminating in a short, angulate tip . . . ***arcuata*** sp. nov. (p. 227)

– D.A.9 (fig. 91) with arc (ARC.) above subapical lobe short and shallow, almost indistinguishably merging with apical lobe (AP.L.) so that entire apical region truncate, not lobate, on anterior margin. Ford's sclerite with thumb (fig. 97, THM.) about twice as high as long. Lower arm (L.A.) of securifer with apex acuminate
thurmani sp. nov. (p. 244)

18 Mesal genitalic ridge of tergum 8 (fig. 139, M.R.8) consisting primarily of a conspicuous, short, horizontal, shallowly arched sclerotization; with anterior vertical portion represented only by a faint dorsal arm and ventral arm inapparent
rhaeba (Jordan, 1926) (p. 257)

– Mesal genitalic ridge of tergum 8 (figs 27, 32, 84, M.R.8) with a well developed vertical branch and this usually more sclerotized than horizontal fork; lacking the conspicuous arched, tanned ridge 19

19 Sternum 7 with subventral sinus not resembling a notch, even at base (figs 26, 31, 124, 7 S.), its dorsal margin sloping away from ventral at an angle exceeding more than 75° 20

– Sternum 7 with subventral sinus notch-like, at least at base (figs. 32, 40, 41, 7 S.), its dorsal margin sloping at angle less than 60° and often paralleling ventral one for at least ⅓ length of latter 21

20 Sternum 7 (figs 26, 30, 7 S.) with dorsal portion of caudal margin (at level of spiracular fossa) sloping ventrad at an angle of about 60° from vertical. Caudal margin fairly evenly rounded (not produced into a lobe) at junction with upper margin of ventral sinus. Tergum 8 (fig. 31, 8 T.) with a ventrocaudal lobe
dryadosa sp. nov. (p. 215)

– Sternum 7 (fig. 124, 7 S.) with caudal margin nearly perpendicular at level of spiracular fossa. With a caudal, short submedian lobe. Tergum 8 (fig. 117, 8 T.) lacking a ventrocaudal lobe . . . . **veruta** sp. nov. (p. 252)

21 Sternum 7 with dorsal margin of subventral sinus sloping dorsocaudad from near base of sinus instead of paralleling ventral margin for ⅓ or more length of latter (figs 40, 130, 7 S.) 22

– Sternum 7 with a true subventral notch (figs 41, 49, 118, 7 S.), dorsal margin paralleling ventral for ⅓ or more of its length 23

22 Perula of bursa copulatrix (figs 40, 137, P.B.C.) with ventral ½ dilated so that ventral ⅓ twice as broad as dorsal ⅓. Paragenital morion (fig. 40, PG.M.) represented by a turned, narrow, U-shaped arc near P.B.C. Glandula vaginalis (G.VG.) single. Ventrocaudal lobe of tergum 8 (8 T.) somewhat longer than broad at base
javana (Jordan, 1933) (p. 256)

– Perula of bursa copulatrix (fig. 118, P.B.C.) elongate, scarcely broader subventrally than subdorsally. Paragenital morion near P.B.C. not tanned. Glandula vaginalis (G.VG.) preceded by an accessory "gland" (fissure) or a part of paragenital morion. Ventrocaudal lobe of 8 T. short, broad and apically blunt; its length less than breadth of base . . . . **loncha** (Jordan, 1926) (p. 255)

23 Perula of bursa copulatrix vermiform (figs 78, 84, P.B.C.), not appreciably broader at middle than near ends. Paragenital morion (PG.M.) large, appearing as a broad, U-shaped loop of stout coils extending from ventral region of P.B.C. to lower portion of sternum 9 (9 S.) 24

– Perula of bursa copulatrix ovoid (figs 32, 41, 102, P.B.C.), more dilated at middle than at ends. Paragenital morion (PG.M.) reduced, not represented by a broad loop of stout coils 26

24 Upright branch of mesal genital ridge of 8 T. (figs 79, 85, M.R.8) in oblique position, and caudal fork sloping ventrocaudad at angle of 45°. Caudal margin of P.B.C. flattened . . . . **limi** sp. nov. (p. 242)

– Upright branch of mesal genitalic ridge of 8 T. (fig. 78, M.R.8) subvertical and caudal fork nearly horizontal. Caudal margin of P.B.C. shallowly convex
phangi sp. nov. & subsp. nov. 25

25 Sinus above ventral lobe of sternum 7 (fig. 75, 7 S.) definitely shorter and narrower than lobe below it. 7 S. scarcely concave above submedian lobe. Paragenital morion with a tanned chord along ventral margin of inner core, near anterior margin of loop, but lacking a transverse rod-like sclerotization in the area
phangi tana subsp. nov. (p. 242)

– Sinus above ventral lobe of 7 S. (fig. 76) subequal to lobe below it. 7 S. fairly deeply concave above submedian lobe. Paragenital morion (fig. 78, PG.M.) with a transverse rod-like sclerotization near anterior margin of loop, instead of a ventral one
phangi phangi sp. nov. (p. 240)

26 Ventral, vertical fork of mesal genitalic ridge of tergum 8 (figs 32, 60, 62, M.R.8) with tanned portion as long as, or longer than, dorsal branch. Horizontal branch equally long. With a rod-like, tanned, narrow loop of paragenital morion (fig. 32, PG.M.) in line with and just caudad to base of perula of bursa copulatrix (P.B.C.) ***robinsoni*** subspp. 27

– Ventral, vertical fork of M.R. 8 (figs 41, 102) definitely shorter than dorsal branch, and horizontal branch equally short. Paragenital morion (PG.M.) lacking a rod-like, narrow loop near base of P.B.C. 30

27 Labial palpus extending beyond base of fore-trochanter. (Sarawak) ***robinsoni peregrinata*** subsp. nov. (p. 235)

– Labial palpus extending at most to apex of procoxa 28

28 Dorsal wall of vagina (figs 32, 59, VAG.) with 1–3 bead-like thickenings distad of glandula vaginalis (G.VG.) (Malayan peninsula) ***robinsoni robinsoni*** (Roths., 1905) (p. 233)

– Dorsal wall of vagina (figs 62, 64, VAG.) lacking bead-like thickenings distad of G.VG. 29

29 Ventral lobe of 7 S. (fig. 62, 7 S.) definitely longer than sinus above it[9]; with only 2 bristles on the lobe (but 1 or 2 subventrals immediately preceding it). (Java) ***robinsoni bogora*** subsp. nov. (p. 235)

– Ventral lobe of 7 S. (fig. 64, 7 S.) subequal to lobe above it; with 3 bristles on lobe. (Tioman Island) . . . . . ***robinsoni tiomanica*** subsp. nov. (p. 236)

30 With an accessory "gland" or fissure in dorsal wall of vagina, distad of glandula vaginalis (fig. 41, G.VG.). With a pair of parallel, short, tanned arcs or chords at dorsocaudal portion of duct of bursa copulatrix (D.B.C.) and another above tip of G.VG. . . . . ***angustata*** sp. nov. (p. 227)

– Lacking both an accessory "gland" distad of glandula vaginalis (fig. 102, G.VG.) and the sets of tanned chords near D.B.C. and G.VG. . ***thurmani*** sp. nov. (p. 244)

B. **Lentistivalius** gen. nov.

Diagnosis. Relatively unmodified species with: (1) Labial palpus (excluding palpiger) (fig. 140) 5-segmented. (2) First preantennal row of bristles quite or actually near frons. (3) Metatibia (figs 149, ♂; 151, ♀) with at most 2 stout dorsomarginal bristles in notches and with subdorsals unmodified and thin. (4) Movable finger (fig. 143, F.) long and narrow, with a well developed stiva (STV.). (5) Sternum 9 with distal arm (figs. 144, 145) clavate and with dilated subapical region armed with marginal spiniforms. (6) Ford's sclerite of aedeagus (fig. 148, F.SC.) with alpha-portion (figs 152, 154, ALPH.) highly developed, apically pointed and often with medial portion approximating the letter "M." (7) Crochet with body (B.CR.) and process (CR.P.) together suggesting a broad letter "U" in appearance. (8) Crochet with only narrow ventral elements linking sclerite with aedeagal pouch and hence lacking a conspicuous quasi-crochet. (9) Phylax (PHY.) slender. (10) Sclerotized inner tube (S.I.T.) of moderate length and lacking specialized armature or spurs. (11) With hood (HD.) and its deltoid flap (DEL.FL.) covering most of lateral surfaces of endchamber. (12) Female tergum 7 with lobe below antepygidial bristles (fig. 156, L.L.7) relatively short, not acuminate. (13) Spermatheca (SP. and fig. 158) at most with a very short dorsocaudal peak. (14) Mesal genital ridge of tergum 8 not developed. (15) Tanned portions of paragenital morion somewhat reduced (fig. 160, PG.M.) rather indistinct.

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[9] Care should be taken that the ventral lobes are the same in appearance on both upper and lower sides of the specimen, for that indicates that the specimen was not distorted in mounting. If, on the other hand, one side is smaller than the other, the possible discrepancies should be considered in interpreting this couplet.

GENERIC DESCRIPTION.[10] Anterior margin of head (figs 140, ♂; 141, ♀) only slightly curved below level of median sensory crater; head relatively short and high, about thrice (or somewhat more) as high (from vertex at falx to ventral margin) as long at level of uppermost bristle of row II in ♂; about 2·5–3·0 times in ♀. Ventral margin of head below eye biconvex, the 2 lobes overlapping slightly at this level. Generally with 4 rows of fairly narrow bristles and with a few "supernumerary" bristles. Labial palpus with fifth (ultimate) segment not reaching beyond procoxae. Dorsal margin of pronotum short, generally about ½ length of dorsal spines of comb (subequal to spines in *aestivalis* Jameson & Sakaguti, 1954). Mesonotum (fig. 142, MSN.) with 1 or 2 pseudosetae per side, usually subdorsal. First segment of metatarsus about 1·45 times length of second and nearly thrice length of third (which is subequal to fifth); about 2·4 times length of first segment of protarsus. Fourth vinculum (fig. 159, VC.4) usually projecting forward as a short rod. Terga 2–4 or 5 with a short subdorsal spiniform. Unmodified abdominal terga with 2 rows of bristles, preceded by a group of a few small subdorsals. Spiracular fossae of these segments broadly sagittate. Basal abdominal sternum with a few proximal submedian bristles in ♂, in ♀ with additional bristles reaching near middle of segment (fig. 159). Female with modified bristles of tergum 7 (fig. 156, U.M.B., L.M.B.) not closely resembling antepygidials (A.B.); only 1 such lower modified bristle and this not strongly displaced. Tergum 7 lacking an appreciable dorsal lobe in ♂ (fig. 147, 7 T.); in ♀, lower lobe (L.L.7) quite short, and upper one (U.L.7) particularly so.

Male. Sternum 8 (fig. 147, 8 S.) very large, nearly 1·5 times as long (near ventral margin) as high; unmodified, and lacking close-set or spiniform ventral bristles. Manubrium (figs 143, 146, MB.) broad; with ventral margin biconvex near middle. Bay of manubrium (B.MB.) extending to near apex. Immovable process of clasper (P.) with apex short and broad, subrounded or blunt. Conical process (C.P.) of clasper fairly broad, 3–5 times as tall as broad at middle. Movable finger (F.) long and thin; about 6–7 times as long (from level of apical margin of P.) as broad at middle of distal fringe (D.FR.). Stiva (STV.) long and narrow. D.FR. with about 4–5 well separated, long and relatively thin bristles; wholly or mainly on upright portion of shaft of F., proximad to curve of the stiva. Fulcral sclerite (F.S.) higher (longer) than broad; subvertical; broadest at dorsal end. Proximal arm of sternum 9 (P.A.9) in subvertical position; gradually broadening from base to near apex, where it may dilate considerably. Distal arm of sternum 9 (D.A.9) nearly length of P.A.9; widening at apical fourth to sixth, at least caudally (ventrally); with that margin bearing a subapical group of spiniforms or short, stout bristles of decreasing lengths (towards apex). Clava of D.A.9 with a lateral supramedial flap (SUP.FL.) bearing small marginal bristles, recalling *Medwayella* (but D.A.9 lacking other specialized features of *Medwayella*).

Aedeagal apodeme (fig. 148, AE.A.) resembling manubrium for most its length though perhaps slightly narrower; lacking an apical appendage. Lateral laminae (L.LAM.) well sclerotized only anteriorly; ventral and caudal portions often very lightly tanned, indistinct. Aedeagal pouch well tanned ventrally (fig. 152, AE.P.-V.), but less so laterally (AE.P.-L.); unsclerotized at base and girdle hence not clearly demarcated; lacking obvious sclerotized connections with crochet process (CR.P.) except for a tail-like ventral process at the base of CR.P. and narrow ventral elements (*cf.* fig. 153, ventral aspect) and therefore lacking a quasi-crochet (*cf.* figs 22, 23, Q.C.). Hood (HD.) without notch or sinus, although at times (fig. 155) concave ventrally; covering most of endchamber; its deltoid flap (DEL.FL.) not produced dorsally into an apical acuminate process. Anterior margin of DEL.FL. well caudad of fulcrum (AE.F.); caudodorsal origin near cephalodorsal angle of Ford's sclerite (F.SC.) rather than upper margin of body of crochet (B.CR.). Lateral lobes (L.L.) greatly reduced; inapparent. Sclerotized inner tube (S.I.T.) sub-horizontal; about 4–6 times as long as broad at middle; lacking dorsal or ventral spurs or other specialized armature. Ford's sclerite (F.SC.) very large and constituting dominant sclerite in endchamber, and with alpha (ALPH.) and securifer (SEC.) components fused and distinctions apparent only at margins (*cf.* fig. 153, ventral aspect). ALPH. a major component of F.SC., and its dorsal, ventral and apical margins with characteristic shapes in various species. Securifer (SEC.) comparatively reduced (in lateral aspect); often produced into an apical spur. Phylax (PHY.) fairly long and narrow, somewhat crescentic in shape, extending from near base of CR.P. to near ventral margin of F.SC. and apex of pivotal ridge (PIV.R.), which is lightly tanned. Pivotal chord (PIV.CD.) weakly sclerotized. Crochet boomerang-shaped or broadly U-shaped; body of crochet (B.CR.) subvertical and crochet process (CR.P.) sub-horizontal. Aedeagal fulcrum (AE.F.) quite narrow. Crescent sclerite (C.S.) moderately long; satellite sclerite (SAT.S.) relatively so; latter overlying base of S.I.T., i.e., appearing as if "within" it. Vesicle (V.) lightly tanned. Third apodemal rod (AP.R.) of endophallus not particularly well developed. Caverna spiculosa (CAV.SPIC.) long, commencing subdorsally but at about level of base of fulcrum.

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[10] The genus is compared with *Medwayella* gen.nov., *q.v.*, and the differences are stressed; similarities are generally omitted.

Female. Spermatheca (figs 156, SP. and 158, 161) longer than broad; bulga (B.) with internal striae; lacking a truly distinct peak; but at times with a short dorsocaudal bulge. Hilla (H.) with an apical papilla (PAP.); base inserted fairly deeply into bulga, protruding element therefore appearing relatively broad in relation to length; internal portion with striae. Duct of spermatheca (D.SP.) bearing internal sclerotized rings at least near dilated portion (DIL.P.). Dorsal region of perula of bursa copulatrix (P.B.C.) associated with 2 sclerotized rod-like or dot-like bodies. Duct of bursa copulatrix (D.B.C.) lightly tanned. Paragenital morion (fig. 160, PG.M.) somewhat reduced; inconspicuous and rather ventral in position, near apical region of bursa copulatrix. Sternum 7 (figs 156, 160, 7 S.) with a subventral sinus. Ventral anal lobe (V.A.L. and fig. 157) with base short; apical margin fairly long, somewhat sinuate; with a gap between submesal and subapical groups of bristles. Anal stylet (A.S.) fairly long and narrow and lacking long subapical bristles. Tergum 8 (8 T.) lacking a conspicuous lobe at ventrocaudal corner. Mesal genitalic ridge of tergum 8 undeveloped. Spiracular fossa 8 (8 SPC.) medium-sized; upright portion ovate. Sternum 8 (8 S.) flask-shaped and with short apical bristles.

The type of the genus is *L. vomerus* sp.nov., described below. Here also belong the "*Stivalius ferinus*-group" of Smit (1958), viz., *ferinus* (Rothschild, 1908), a parasite of shrews on the Indian subcontinent, Ceylon and South China; *insolli* (Traub, 1950), a flea of birds in the mountains of Malaya; *aestivalis* (Jameson & Sakaguti, 1954) infesting *Apodemus speciosus*, a wood-mouse in Japan; and *alienus* (Smit, 1958) stated by the author to be a parasite of rodents, and occurring in East and Central Africa.

COMMENT. The generic name is derived from the Latin term *lentes*, meaning *flexible*, and refers to the remarkable facility of this genus to adapt to a broad variety of hosts, in widely separated areas, as indicated above. This point is discussed further below in the second article in the series, dealing with convergent evolution, and in the third, which concerns zoogeography.

1. **Lentistivalius vomerus** sp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-19249) ex *Tupaia montana*; NORTH BORNEO (EAST MALAYSIA, Sabah): Mt. Kinabalu, Tenompak; elev. 4500 ft; 16.VIII.1953; Coll. R. Traub for U.S. Army Medical Research Unit (Malaya). Paratypes, all from North Borneo (East Malaysia, Sabah) as follows:

♂	♀	Host	Locality, Date and Collector		
99	75	*Tupaia montana*	Mt. Kinabalu, vicinity of Tenompak; elev. 4500–5500 ft;	July 1, 1951	R. Traub
				August, 1953	R. Traub
				May, 1952	J. R. Audy
				Feb.–Mar. 1964	Lord Medway & Cambridge Univ. Exped.
				Dec. 1965	Lim Boo Liat & D. Heyneman for G. W. Hooper Foundation
3	1	,, ,,	Mt. Kinabalu, vicinity of Mari Parei; elev. 4000–5100 ft;	24–25.VIII.53	R.T.
1	–	,, ,,	Mt. Kinabalu, Lumu Lumu; elev. 6300 ft	23.VII.1951	R.T.
–	3	,, ,,	Mt. Kinabalu, Kamborangah; elev. 7200 ft	3.VI.1952	J.R.A.
6	4	,, ,,	Mt. Trus Madi, Pampang, Ulu Kaingaran; elev. 4000 ft	19.VII–7.VIII.53	J.R.A.
1	–	,, ,,	Mt. Trus Madi; elev. 7500 ft	30.VIII.1956	Cambridge U. Exped.
5	3	*Dendrogale melanura*	Mt. Kinabalu, Lumu Lumu; elev. 6300 ft	21.VII.1951	R.T.
–	1	,, ,,	Mt. Kinabalu, Mari Parei; elev. 5100 ft	25.VIII.1953	R.T.
–	1	,, ,,	Mt. Kinabalu, Tenompak; elev. 4500 ft	30.VIII.53	R.T.

♂	♀	Host	Locality, Date and Collector	(continued)
3	–	,, ,,	Mt. Trus Madi, Pampang, Ulu Kaingaran; elev. 4000 ft 1.VIII.1953	J.R.A.
–	1	,, ,,	Mt. Trus Madi, Kidokarok; elev. 5000 ft 3.IX.1956	Cambridge U. Exped.
2	1	*Dremomys everetti*	Mt. Kinabalu, Tenompak; elev. 4500 ft 16.VII.51, 31.VIII.53	R.T.
1	1	,, ,,	Mt. Kinabalu, Tenompak; elev. 9800 ft Dec. 1965	L.B.L.
1	1	,, ,,	Mt. Kinabalu, Lumu Lumu; elev. 6300 ft	R.T.
2	1	,, ,,	Mt. Trus Madi Aug.–Sept. 56	Cambridge U. Exped.
1	1	,, ,,	Mt. Trus Madi, Pampang, Ulu Kaingaran; elev. 4000 ft July-Aug. 53	J.R.A.
–	3	*Hylomys suillus*	Mt. Kinabalu, Tenompak; elev. 4500–5000 ft 16.VII.59, 12–20.VIII.53	R.T.
1	–	,, ,,	Mt. Kinabalu, Mari Parei; elev. 5100 ft 25.VIII.53	R.T.
3	–	*Rattus alticola*	Mt. Kinabalu, Tenompak; elev. 5500 ft 16.VII.1951	R.T.
–	1	,, ,,	Mt. Kinabalu, Mesilau Base Camp 10.II.1964	L.M.
–	1	*Rattus whiteheadi*	Mt. Kinabalu, Tenompak; elev. 5500 ft 19.VII.1951	R.T.
2	2	*Rattus* sp.	Mt. Kinabalu, Bundu Tuhan; elev. 4000 ft 26.V.1952	J.R.A.
1	1	,, ,,	Mt. Kinabalu, Kamborangah; elev. 7200 ft 5.VI.1952	J.R.A.
–	1	*Haematortyx sanguiniceps*	Mt. Trus Madi, Pampang, Ulu Kaingaran; elev. 4000 ft 22.VII.1953	J.R.A.
1	–	Shrike	Mt. Kinabalu, Lumu Lumu, elev. 6300 ft. 23.VIII.1951	R.T.

Holotype (U.S.N.M. number 71609), allotype and five pairs of paratypes deposited in U.S. National Museum. Remaining paratypes distributed as for *M. dryadosa.*

DIAGNOSIS. Close to *L. insolli* (Traub, 1950) (new combination) and even agrees with it in that the dorsal and submedian tanned margins of the alpha-portion of Ford's sclerite (figs 152, 154, ALPH.) are shaped somewhat like the letter "M." Instantly separable in that the new species lacks modifications of the pronotal comb of *L. insolli* which have been cited (Traub, 1969) as being characteristic of bird-fleas, viz.: (1) A large number (about 28 in *L. insolli*) of narrow, quite straight, mainly horizontal, parallel spines in a comb which does not descend over third vinculum. (2) Axis of the bases of the majority of spines in comb slopes anteroventrad. Instead, in the new species, there are only about 20 spines in the pronotal comb (fig 140) and the spines are broader, i.e., no significant gaps between them and yet height of comb is the same—extending to a level just above VC.3; middle 6 spines fairly concave, and axis of the bases of the main spines largely subvertical, not oblique. It has been pointed out (Traub, 1966) that in bird-fleas (and presumably other ectoparasitic insects parasitizing birds) the bristles of the body are longer and thinner than in relatives infesting mammals, and this is also true for *L. insolli* versus *L. vomerus*, e.g., caudoventral bristle of mesepimere 31 times as long as broad at base in the former species and only 23 times in the latter (fig. 142, MPM.).

Further separable from *L. insolli* as follows: (1) movable finger (fig. 143, F.) proportionately much broader in new species, i.e., only 4·4 times as long (from apex of P.) as broad immediately below stiva (STV.), instead of more than 7·6 times (fig. 146). (2) Distal arm of ♂ sternum 9 (D.A.9 and fig. 144) with apical margin ovate, not oblate (fig. 145); margin above subapical spur curved and slanting, not straight. (3) Spermatheca relatively longer and narrower, i.e., about 2·2 times as long as broad at maximum diameters (figs 158, 160) when undistorted, instead of 1·7 times.

Near *L. aestivalis* but instantly separable as follows: (1) Deltoid flap (fig 152, DEL.FL.) virtually squarely meeting ventral margin of hood (HD.) at anteroventral corner instead of being produced into a long, acuminate, curved structure (fig. 155). (2) Crochet process (CR.P.) narrowly ovate, nearly 5 times as long (to middle of base B.CR.) as broad at middle, instead of being trapezoidal and broader, viz., 2·5 times as long as broad. (3) Lobe above subventral sinus of ♀ sternum 7 (fig. 156, 7 S.) at most with a shallow sinus instead of one that virtually equals that below it, so that this region is practically evenly biconcave. Differences from other species of *Lentistivalius* are indicated in the key which follows the description below.

Descriptive notes.[11] Head (figs 140, ♂; 141, ♀). With preantennal portion of head of ♂ about 2·4 times as high as long at level of eye-bristle and slightly more than thrice as high as long at level of uppermost bristle of row II; in ♀ comparable figures are 2·3 and 3. With preantennal bristles in 4 rows except for a fair-sized supernumerary between rows II and III. Labial palpus with apical segment 1·7 times length of penultimate (fourth); extending to about apex of procoxa.

Thorax. Pronotum (fig. 140) narrow; dorsally with spines of comb about 2·5 times length of notum; with 2 rows of bristles, but first row highly abbreviated. Pronotal comb with a total of about 20 spines, of which, in ♂, numbers 2 – 8 per side (counting dorsalmost as number 1) are slightly convex, narrowing gradually from base to apex; bluntly pointed or subovate at apex; bases of middle spines inclined ventrocaudad at an angle of about 20°; spine number 7 the broadest, but only slightly exceeding its mates, about 5 times as long as broad at middle. Mesonotum (fig. 142, MSN.) with 4 rows of bristles; first row abbreviated; those of first 2 rows short; with 1 subdorsal pseudoseta per side. Mesepisternum (MPS.) with oblique row of 4 bristles; dorsalmost (first) of these near middle of caudal margin; slope anteroventrad; first and third bristles long; lowest subventral in position. Mesepimere (MPM.) with 2 rows of 3 long bristles; that near ventrocaudal angle longest. Third vinculum (VC.3) with dorsal margin basally quite flat, distal $\frac{1}{2}$ concave; axis about 35°–45° from horizontal. Lateral metanotal area (L.M.) with external measurements slightly longer dorsally than high, but internal, relatively untanned region somewhat higher than long. Metepimere (MTM.) with 3 rows of 3–4 bristles each and those of last row with intercalaries (usually 2 such between ventral pair of long ones); caudal margin becoming shallowly convex near level of spiracular fossa.

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[11] The species is compared with *M. dryadosa*, *q.v.*, and the differences are stressed; similarities are generally omitted.

Legs. Metacoxa with a group of about 14–16 short, thin, mesal bristles on apical ⅓, anterior to internal rod. With 5–8 submedian lateral bristles in 2 irregular longitudinal rows of profemur. Meso- and metafemora with 4–5 small subdorsal bristles on apical ½; 3 ventromarginals on distal ⅕ and 2 submedians near spiniform member of apical pair of stout bristles. Protibia in ♂ with first (apical) and fifth members of dorsomarginal pair of bristles much shorter and somewhat longer than their mates, hence appearing as "single" bristles, in ♀, with 3 such single bristles between third and fifth pairs, and since first pair is similarly modified, this sex here bears an incipient comb of false spines. Other legs with dorsomarginals paired in usual manner (metatibia, figs 149, ♂; 151, ♀), and only D.M.4 single; ♂ with 3 non-marginal rows of lateral bristles and only 1–2 supernumerary bristles; ♀ with 4 such rows. An apical bristle of mesotarsus I–III and of metatarsus II and III, reaching to middle of succeeding segment. Proportions of tarsi essentially as that cited for *L. insolli* (Traub, 1950). Metatarsus with apical segment with 6 pairs of lateral plantar bristles, but third displaced towards midline (fig. 150).

Abdomen. Basal sternum of ♀ with group of about 7–10 small, thin, lateral bristles commencing near vinculum and extending to about anterior ⅓ and ventral ⅓; in ♂ with at least the bases for about 6 such hair-like bristles, but group nearer to anterodorsal region. Terga 2–5 usually with 1 subdorsal apical spinelet. Spiracular fossae in unmodified terga of ♂ symmetrical and narrowly sagittate (e.g., fig. 147, 7 SPC.); in ♀ shorter and broader and dorsal margin more convex than ventral (fig. 156, 7 SPC.). Representative sterna of ♂ with ventral group of 3 long bristles preceded by a group of 3 smaller ones and 1 more anterior ventromarginal one (e.g., 7 S.). In ♀ (fig. 156, 6 S.) such sterna with 4 bristles in caudal row, but, except for 6 S., uppermost usually small; middle subventral group of 4–6 small ones; anteriormost, 3 or 4. Uppermost antepygidial bristle (A.B.) in each sex somewhat less than half of lower one. Female with only 2 adjacent bristles modified so as to suggest A.B., and only somewhat so, viz., dorsomarginal one (U.M.B.) rather dark and stout, but not displaced; lower one (L.M.B.) fairly close to A.B. but not as long, dark and stout as upper A.B. Dorsal lobe of tergum 7 (U.L.7) not produced caudad above and between bases of A.B.; margin below A.B. (L.L.7) scarcely extending beyond A.B., viz., not truly lobate.

Modified Abdominal Segments—Male. Tergum 8 (fig. 147, 8 T.) slightly more than twice as high as long at middle; somewhat dilated ventrally; not extending below level of base of ventral anal lobe (V.A.L.). Vertical arm of spiracular fossa 8 (8 SPC.) rather more than thrice as high as broad at middle; dilated horizontal section only 1·25 times longer than high or than vertical arm is broad at middle. Sternum 8 (8 S.) nearly twice as long (along ventral border) as high at middle (level of first dorsal bristle); ventral margin sloping towards middle much more than upper, but quite straight for most its length; cephalic margin shallowly concave; caudal margin quite straight. 8 S. with bristles approximately as follows: a dorsomarginal row of 4, commencing just beyond midpoint, where margin starts to curve caudoventrad, and terminating at caudal ⅙ ,the last bristle by far the longest; with 5 subdorsal bristles, arranged 3–2, the first ventral row near midline, the second row oblique and in line with first of dorsomarginals; a horizontal row of 3 along midline, starting at anterior ⅓ and terminating near margin; another horizontal row of 3 just below this, but bases somewhat more cephalad and otherwise symmetrical; a group of 2 subventrals, submedian, in a horizontal row; with 8–10 ventromarginals, or contiguous short bristles, arranged in twos and threes, starting near midline and terminating subcaudally; none of the above bristles anterior to cephalic ¼, and most caudal of midline. Immovable process of clasper (fig. 143, P.) dorsally very broadly and shallowly rounded; with a short dorsomarginal bristle near middle of dorsal margin and another, longer, subapical one near apex of P.; caudal margin very shallowly sinuate distad of marked sinus at base of manubrium (MB.). Conical process (C.P.) about 3·5–4 times as long a broad at middle; caudal margin straight. Movable finger (F.) with portion distad of apex of P. about 5·4 times as broad at level just proximad of curve of stiva (STV.) (*cf.* fig. 1, j k) and 3·7 times as broad at level of apex of C.P.; the difference representing the degree of gradual narrowing of F. from base towards apex. F. with anterior and posterior margins otherwise appearing parallel; anterior margin somewhat convex but becoming slightly concave between proximal and third sensilla of group of 4 (S.G.). Stiva (STV.) fairly long and quite narrow; length (*cf.* fig. 1, measured from k–o to p) about 1·3 times subapical width of F.(j–k) and about $\frac{9}{15}$ of total length of apex of F. (l–p); about thrice breadth of middle of stiva. Distal fringe (D.FR.) of 4 widely spaced, relatively thin, long bristles, commencing at level of middle of F. (above P.) and terminating at level of middle of STV. Fulcral sclerite (F.S.) essentially a right triangle with base and hypotenuse slightly sinuate and with altitude concave and apex blunt; length about 1·7 times breadth at dorsal margin, thrice that at middle and about 7 times that at apex. Manubrium (MB.) fairly broad; length (as measured from base of dorsal margin, where base of F. angles ventrad) about 1·9 times breadth of MB. at anterior ventral bulge; dorsal margin slightly convex to near apex, where it becomes sinuate and fairly straight subapically; ventral margin parallel to dorsal near apex, somewhat sinuate to anterior bulge and here biconvex but sinus between bulges short; caudal bulge longer than anterior; apex slightly upturned; anterior margin, at tip, relatively straight. Tergal apodeme of ninth segment (T.AP.9) relatively narrow; length (to base of F.) nearly 6 times breadth at middle. Proximal arm of sternum 9 (P.A.9) about 6·5 times as long (*cf.* fig. 1, from aa–bb to level of ii) as broad at base (gg–hh); length thrice breadth at bulge of anterior margin at distal ⅓ (dd); 2·2 times breadth at apex (aa–bb). P.A.9 with dorsal (posterior) margin slightly biconcave; anterior margin fairly concave at distal ⅓ (aa–dd) and thereafter quite straight; dorsal margin shallowly sinuate except at corners. Distal arm of sternum 9 (D.A.9 and fig. 144) nearly 6 times as long (ii–qq) as broad at middle; margins sinuate but parallel to above apical ⅓, where caudal margin becomes oblately convex, so that distal portion resembles the head of a mace with posterior and apical margins oblate. Armature of mace-head consisting of marginal spiniforms, as follows: a stout sub-proximal one, above which are 4–5 smaller, paler spiniforms, commencing at middle of distal margin, and below which is 1 fairly long spiniform with a longish subspiniform at base of dilated portion. D.A.9 with a subapical nubbin or short, stout, spur on anterior margin, above a short notch with well tanned margins. Dilated or club-like apex of D.A.9 about 1·4 times as long (from basal subspiniform) as broad at level immediately below subapical notch.

Aedeagus—Lateral Aspect (figs 148, 152, 172). Aedeagal apodeme (fig. 148, AE.A.) with middle lamina (M.LAM.) more tanned than lateral plates (L.LAM.); latter only well sclerotized near anterior end, and ventral and caudal portions semimembranous, indiscrete, with ventral region appearing confused with penis rods. M.LAM. about 4·4 times as long (from anterior edge of crescent sclerite, (C.S.), at base of aedeagal fulcrum, (AE.F.)) as broad at anterior margin of bay of middle lamina (B.M.L.). AE.A. significantly narrowing only at level of anterior edge of B.M.L.; rather resembling MB. in shape but not as broad; apex somewhat upturned. B.M.L. extending to apical ¼. Median dorsal lobe (M.D.L.) sloping dorsocaudad at angle of about 45° commencing at level of AE.F.; straight to even, broad curve at level of Ford's sclerite (F.SC.). Aedeagal pouch (AE.P.) with base very lightly tanned and hence not representing a typical girdle, but with usual elements proceeding dorsad to top of apodeme, near anterior end, and en route blending with extensions of L.LAM. which project ventrad towards fulcrum and which join indistinct ventral margins of L.LAM. from anterior end of apodeme. Ventral wall of pouch (fig. 152, AE.P.-V.) well tanned. Hood (HD.) covering endchamber as a symmetrical cowl whose ventral margin is fairly straight and extends from tip of apices of Ford's sclerite (F.SC.) to apex of crochet process (CR.P.); extended dorsad as the deltoid flap (DEL.FL.) and terminating acutely in subdorsal region at level of basal ¼ of sclerotized inner tube (S.I.T.); dorsal and ventral margins in the main at right angles to cephalic margin. Ford's sclerite (F.SC.) largest (in mass) of sclerites in endchamber; shaped like a broad, low arch with longitudinal axis horizontal. Most conspicuous part of alpha-portion (ALPH.) an M-shaped ridge or thickening whose one leg is long, subdorsal and subhorizontal; opposite leg only about half as long and with cross-bar in the form of a shallow "V", and apical. Distad of the "M," with a bell-shaped dome which is longer than high and terminates apically in an eccentric (ventral) short stalk, contiguous with a caudal acuminate process of the securifer (SEC.) so that tip of F.SC. is bifid. Securifer semi-circular, its lower (anterior) leg a short, fairly blunt lobe. Pivotal ridge (PIV.R.) lightly sclerotized and its chord (PIV.CD.) short, narrow and straight. Sclerotized inner tube (S.I.T.) nearly 7 times as long (from caudal apex of Y-sclerite (Y.S.) to middle of apex) as broad at level of caudal margin of crochet process (CR.P.) and 3·3 times as broad at sub-basal thickening (i.e., at short ventral bulge); axis very slightly arched to short up-curve at apex, where dorsal margin bears a short peak. Crescent sclerite (C.S.) fairly long and narrow; borders at times indiscrete because of unusual degree of tanning of lateral shafts of capsule (L.S.C.) and proximity of relatively large satellite sclerite (SAT.S.). Caudal extremity of C.S., and all of SAT.S., overlying base of S.I.T. Central sclerite (CEN.S.) closely appressed to fulcral medial lobe (FUL.M.L.); the two together appearing as the upper part of an arrowhead. Y-sclerite (Y.S.) conspicuous as a large, sub-triangular sclerite as broad as base of fulcrum and ventral to it, and with a narrow, rod-like fork extending dorsocaudad to above mid-line of S.I.T. at level of apex of C.S. Dorsal virga (D.V.) indistinct. Phylax (PHY.) a crescent whose chord is about 8 times its breadth at middle; lying across middle of S.I.T. so that upper ½ is above S.I.T., with apex near ventral tip (base) of F.SC.; lower ¼ of PHY. below S.I.T. and contiguous with crochet. Body of crochet (B.CR.) terminating at base of F.SC.; clavate, broadest subapically; ventral portion about ½ as broad as upper, as sclerite curves caudad. Crochet process (CR.P.) digitoid, directed caudad and proceeding slightly beyond level of apex of B.CR. With a short spur pointing cephalad and arising from anteroventral angle of crochet and merging with ventral walls of aedeagal pouch. Upper member of penis rods (P.R.) extending to near apex of apodeme; lower members shorter; both paralleling ventral margin of L.LAM. Ventral virga (V.V.) stout; sclerotized to level of about base of AE.P. Third apodemal rod (AP.R.) well tanned to base of AE.P., but apparent for most its length, which equals P.R.

Aedeagus—Ventral Aspect (fig. 153). Hood (HD.) bifid apically. Ford's sclerite with distal ½ consisting of broad, sub-quadrate, right and left components fused near base, at midline, but well separated distad; alpha (ALPH.) and securifer (SEC.) elements forming blended and integral parts of each ½ (and hence here constituting merely topographic terms useful in taxonomic distinctions). Basal ½ of F.SC. semicircular. Deltoid flap (DEL.FL.) covering lateral ⅙ of ventral surface. Phylax (PHY.) with ventral portion of each straddling sclerotized inner tube (S.I.T.) and sloping towards midline dorsally so that apices are virtually contiguous, above S.I.T. and here connected by a membrane; dorsal region stouter (from lateral surface towards mesal) than ventral. Wall of aedeagal pouch with ventral extensions (P.W.EX.) leading to floor of base of CR.P. Lateral lobes so ventral in position they appear like mesal structures. S.I.T. dilated subapically. Satellite sclerite (SAT.S.) along midline; well distad of base of S.I.T. and mesad of apices of crescent sclerites (C.S.). Lateral shafts of capsule (L.S.C.) relatively broad as well as long. Vesicle (V.) broad. Y-sclerite with ventral components broadly triangular with winged angles at base, serving as floor of capsule; more dorsal fork with symmetrical, broad, ovoid projections extending more mesad. Fulcral lateroventral lobes (FUL.L.L.) short, fairly widely separated. Caverna spiculosa (CAV.SPIC.) very long, somewhat fusiform, and occupying much of breadth of apodeme.

Female. Sternum 7 (fig. 156, 7 S.) about 1·5 times as high as long at maximum diameter (i.e., level of maximum curvature of median lobe on caudal margin); anterior margin very shallowly convex; dorsal margin oblate; caudal margin with a subventral short sinus which is scarcely more than ⅓ of height of lobe beneath it. 7 S. with lobe above this sinus somewhat concave (at times more so than in figure) but soon straightening and sloping antero-dorsad from level of apex of ventral anal lobe (V.A.L.); margin rather concave from level of dorsal part of sensilium (SN.) to upper part of spiracular fossa 8 (8 SPC.). 7 S. with vertical caudal row of 4 long bristles, of which 1 is ventral and 1 subventral, about at level of middle of ventral lobe; 1 slightly above level of sinus and uppermost above third by distance equal to mouth of sinus; this row removed from caudal margin by distance equivalent to ½ length of lowest bristle. This row preceded by a vertical group of about 10 smaller bristles, most of which are in a line but some subventrals displaced caudad, as is a fairly long ventromarginal. Latter group preceded by about 10 bristles in 2 short, irregular, subventral rows of 3–4 and 4–5, plus 1 or 2 marginals or submedians out of line. Tergum 8 (8 T.) with caudal margin straight and oblique to short lobe at ventrocaudal angle; with 2 rows of small bristles, usually 2–5, immediately before vertical portion of 8 SPC.; with a subventral, horizontal row of 3 fairly long bristles, preceded by 1 small one and with the caudalmost inserted before apex of sternum 8 (8 S.); with an oblique subvertical row of 3 bristles at level of base of V.A.L., of which uppermost is at level of upper member of ventral genital pair at caudal margin and lowest in line with ventrocaudal lobe; with 2 vertical rows of more anterior bristles; the first (anteriormost) of 3 small ones in line with ventral base of 8 S. and lowest of which was cited above as preceding subventral horizontal row; the second, of 3 small submedians, of which ventralmost is in line with first member of subventral horizontal row; third row of 4 submedians in line with second large member of subventral horizontal row. 8 SPC. with vertical portion broadly ovate, about twice as high (including section overlapped by horizontal arm) as long at middle; horizontal portion with tanned area about 2·2 times as long as broad at base. Dorsal anal lobe (D.A.L.) with a dorsomarginal row of 3 or 4 bristles; and 1–2 tiny ones contiguous with base of sensilium (SN.); caudalmost dorsomarginal very long; with a subdorsal row of 3, of which caudalmost is long, in line with last dorsomarginal and above base of anal stylet (A.S.); with a pair of subventrals immediately preceding long bristle ventrad to base of A.S.; with 2–3 small, scattered submedians. A.S. about 4 times as long as broad at middle; with a very small subapical bristle dorsal and ventral to base of apical long bristle. Ventral anal lobe (V.A.L.) angulate, with anterior margin less than $\frac{3}{8}$ length of ventral margin; with 3 groups of ventromarginal bristles—a subequal but longish pair at anteroventral angle (at times represented by a single bristle); a long one at anterior fourth (at times paired here, e.g., when first is single), and a long pair on a short mesal flap at caudal third or fourth. Spermatheca with outlines variable, depending upon position in slide-preparation. Typically (fig. 156, SP. and fig. 158), as when seen in lateral aspect, with bulga elnogate-oval, approximately twice (or 2·2 times) as long (maximum diameter) as broad in middle. Atypical appearance shown in figs 160 and 161, and latter particularly misleading, for bulga seems only 1·7 times as long as broad. Bulga typically with ventral margin fairly flat except for anterior up-curve at level of apex of lower margin of internal portion of hilla (H.); dorsal margin anteriorly quite straight but with a subtruncate, short posterior bulge; caudal margin convex. Hilla (H.) inserted into lumen of bulga for about $\frac{1}{2}$ its length; external portion recurved at middle and apex rather flat, oblique below the apical papilla (PAP.); internal portion longer than breadth (inner measurements) at middle; of fairly uniform breadth to near apex. Bursa copulatrix with a pair of characteristic tanned, short rods or ill-defined thickenings flanking apex of perula (P.B.C.), one anterior and one posterior, at base of sac of bursa (SAC.). P.B.C. narrow, unmodified, scarcely differentiated from duct (D.B.C.) below it. Dilated portion of bursa (DIL.P.) weakly tanned and subequal in length to dorsal part of SAC. Duct of spermatheca with internal striae usually visible near entrance into SP. and near DIL.P. Paragenital morion (PG.M.) reduced to an indefinite semimembranous area near upper wall of vagina (VAG.) at genital orifice and overlying ventral portion of bursa; with elements lying anterior to latter. Glandula vaginalis (G.VG.) short, broad and indistinct, partially underlying expanded base of apical wall of bursa. Duplicatura vaginalis (D.VG.) indiscrete, at base of vertical portion of SAC., which broadens at level of vagina, anterior to orifice of bursa copulatrix.

HOST-RELATIONSHIPS AND DISTRIBUTION AND OTHER COMMENTS. The name *vomerus* is derived from the Latin word for plough-share and was selected not only because the shape of the movable finger resembles a plough-handle, but because Ford's sclerite, as seen in dorsal or ventral aspect, suggests the share of the plough, with the elongate crochet-processes serving as handles, while, in lateral aspect, the crochet-processes themselves suggest the share as seen from the side.

Lentistivalius vomerus sp. nov. is obviously common in the mountains of North Borneo, especially at elevations of about 4000–6300 ft, where it parasitizes primarily *Tupaia montana* but apparently also infests other small mammals in the same habitat, e.g., *Dendrogale* (a tupaiad), ground-squirrels and rats, on or near the forest-floor. It was collected on occasion at higher elevations, even above 9000 ft. The absence of records from tree-squirrels on Mt. Kinabalu and Mt. Trus Madi is significant, since I examined at least 50 such *Callosciurus* in the former area, and Lim Boo Liat, M. Nadchatram, J. R. Audy and others of our colleagues also collected fleas from tree-squirrels in both regions.

ILLUSTRATIONS

140. Head and prothorax (♂)
141. Head (♀)
142. Meso- and metathorax (♂)
143. Clasper and segment 9
144. Distal arm of sternum 9
147. Modified abdominal segments (♂)
148. Aedeagus
149. Metatibia (♂)
150. Segment 5 of metatarsus (♂)
151. Metatibia (♀)
152. Apical region of aedeagus (lateral)
153. Apical region of aedeagus (ventral)
156. Modified abdominal segments (♀)
157. Anal lobes and stylet (♀)
158. Spermatheca
159. Abdominal segments 2 (♀)
160. Spermatheca and genitalia
161. Spermatheca (variation)
172. Apical region of aedeagus

2. KEY TO THE KNOWN SPECIES OF **LENTISTIVALIUS** gen. nov.

1 Pronotal comb with a total of about 26–28 spines, close-set, their bases contiguous; spines narrow, about 6·5 times as long as broad at middle; most of spines parallel and similar in shape. (Malayan bird-fleas)[12] . . . . . ***insolli*** (Traub, 1950)

Pronotal comb (fig. 140) with about 18–20 spines; spines distinctly separated at bases; generally broad—about 5·4 times (or less) as long as broad at middle (narrow in *L. ferinus*, but not close-set); spines variable in shape and inclination, at least regarding dorsal versus ventral ones. (From mammals; in other areas) 2

2 First preantennal row of bristles spiniform in shape. With 4–5 spiniforms bordering frontal margin of head. Pronotal comb[13] with spines mainly concave dorsally and with apices broad and rounded. (On shrews; Indian subcontinent and southern China) . . . . ***ferinus*** (Rothschild, 1908)

– First preantennal row of bristles unmodified; only ventral 2 bristles bordering frontal margin (fig. 140). Pronotal comb with spines fairly straight, apices narrowed, pointed (fig. 140) or angled.[14] (Generally on tupaiads or rodents; Africa or Asiatic-Pacific islands) 3

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[12] See next article in series for illustrations of pronotal combs of other *Lentistivalius*, viz., fig. 18 for *insolli*.

[13] See fig. 15 in next paper.

[14] See fig. 16 in next paper.

3 With only 1 row of bristles on pronotum. Distal arm of ♂ sternum 9 lacking a subapical spur on anterior margin. ♀ sternum 7 with subventral sinus near middle of lower ½ of caudal margin. ♀ spiracular fossa 8 with vertical portion relatively broad, viz., less than twice as long as broad at middle. (Africa) . **alienus** (Smit, 1958)

– With 2 rows of bristles on pronotum (fig. 140). Distal arm of ♂ sternum 9 with an anterior subapical spur (figs 144, 145). ♀ sternum 7 with subventral sinus much closer to ventral margin than to middle of caudal margin (fig. 156, 7 S.). ♀ spiracular fossa 8 with vertical portion more than twice as long as broad at middle. (Borneo and Japan) 4

4 Deltoid flap of aedeagus with a ventrocaudad-directed acuminate process arising at anteroventral corner (fig. 155, DEL.FL.). Crochet-process (CR.P.) only about 2·5 times as long as broad at middle. ♀ sternum 7 definitely biconcave, upper sinus on caudal ½ taller than and nearly as deep as subventral one. (Japan) **aestivalis** (Jameson & Sakaguti, 1954)

– Deltoid flap of aedeagus relatively squared at anteroventral corner, lacking an acuminate projection (fig. 152, DEL.FL.). Crochet-process (CR.P.) nearly 5 times as long as broad at middle. ♀ sternum 7 with only one distinct sinus, and that subventral (fig. 156, 7 S.). (N. Borneo) . . . . **vomerus** sp. nov. (p. 272)

C. **Stivalius** Jordan & Rothschild, 1922, *Sensu Strictu*

Stivalius Jordan & Rothschild, 1922. Ectoparasites 1 : 249–250. Type of genus: *S. ahalae* (Rothschild, 1904).
Stivalius, Holland, 1969, Mem. ent. Soc. Canad. No. 61 : 14.

A major contribution to our understanding of *Stivalius s. lat.* was made by Holland (1969) when he created seven new genera based upon New Guinean species and described and illustrated new species in these taxa. In this connection, Holland aptly and capably defined *Stivalius s. str.*, thereby presenting a standard by which his new genera could be compared, and easing the work of those who followed him. In order to facilitate evaluation and characterization of the new genera described above in the present opus, *Stivalius* Jordan & Rothschild *s. str.* is now redescribed, citing aedeagal and some other characters not previously mentioned, so that direct comparison with the new genera in the present paper is feasible. A new subspecies of *S. cognatus* Jordan & Rothschild, 1922, is described to illustrate the typical features of the taxon.

Diagnosis. Instantly separable from related taxa by: (1) the elongated sclerotized inner tube (figs 170, 173, 174, S.I.T.) which is 9–30 times as long as broad at middle and arched at least for apical ½, and (2) the bursa copulatrix, which appears either grossly swollen throughout and coiled for most its length (fig. 176, B.C.) or else the apical ½ is folded upon itself (fig. 162) (*S. phoberus* Jordan & Rothschild, 1922). Also characteristic as follows: Movable finger (fig. 165, F.) long and narrowed with well developed stiva (STV.). Conical process (C.P.) broad. Ford's sclerite (figs 170, 173–174, F.SC.) large—longer than adjacent sclerites, narrowed subapically and terminating in 1 or 2 hook-like projections. (This fact, and elongated S.I.T., probably account for the noteworthy absence of ventral paramere-like processes, e.g., the crochet lacks a caudad-directed arm.) S.I.T. bearing a distinctive basal sclerite (L.W.AR.). Distal arm of sternum 9 (figs 167–169, D.A.9) apically with a short lobe (A.LB.9) bearing bristles, and a mesal apicocaudal flap or expansion (AC.F.9) bearing marginal subspiniforms. Labial palpus 5-segmented (excluding palpiger). Tibiae with some stout subdorsal setae next to, or incorporated within, dorsomarginals so that some of notches appear to contain 3 bristles. Full-length false tibial combs lacking and rarely with even the appearance of one on apical ½.

GENERIC DESCRIPTION. Head in general resembling *Medwayella* and *Lentistivalius* but somewhat longer and bearing more bristles. Head rounded and somewhat recurved in ♂ (fig. 164); "frontal" region here somewhat less than thrice as high (vertex to ventral margin) as long at level of uppermost bristle of row II, and about twice as long at level of eye bristle; in ♀, corresponding figures are about 2·5 and 1·6–2 times, respectively. With head-bristles slender; preantennals in 4 rows but with several supernumeraries, which may appear like a fifth row. Eye large, reniform, with sinus ventral, subcaudal and subventral in position, just above apex of procoxa. Eye bristle (E.B.) inserted above level of eye, but in ♂, with caudalmost bristle of row IV just in front of eye. Ultimate (fifth) segment of labial palpus reaching apex of procoxa, or nearly so. With 3 rows of postantennal bristles, plus the usual 1 midway between last 2 rows, near antennal groove.

Pronotum dorsally subequal to, or slightly exceeding, length of adjacent spines of comb; with 2 rows of bristles, first row incomplete; comb with a total of 22–24 spines, and these narrow, somewhat oblique and bluntly pointed. Mesonotum with 4 regular rows of bristles but anteriorly crowded with smaller bristles that may constitute 1–2 additional rows; the greater number occurring in ♀, with 1 subdorsal pseudoseta. Metanotum with 3 regular rows of bristles plus a more anterior incomplete row. Mesepisternum with about 4–5 bristles; mesepimere 5-6. Lateral metanotal area somewhat higher than long; with a dorsocaudal long bristle. Metepisternum with a dorsocaudal bristle. Squamulum short and broad in some species; long and thin in others. Metepimere usually with 12–13 bristles in 3 rows, and some of last row accompanied by 1–2 small intercalaries. Tibiae with 7 groups of stout dorsomarginal bristles (including apical one); in pro- and mesotibiae, usually with 4 groups containing 3 stout bristles each. Metatibia with at least 5 distinct notches containing dorsomarginals and these generally with 2 stout bristles and with 1–2 of subspiniform type below the notch; lacking full-length false combs, and in only one species (*S. aporus* Jordan & Rothschild, 1922) does even apical ½ appear comb-like. Fifth tarsal segment with 6 pairs of plantar bristles, of which fourth pair (from base) somewhat displaced towards midline; in pro- and mesotarsi, first pair may also be slightly displaced. None of tarsi with apical bristles extending beyond middle of next segment (except perhaps for distalmost of fringe of segment 1 of protarsus in both sexes). Proportions of tarsal segments essentially as that noted for *Medwayella dryadosa*.

First abdominal tergum with 4 rows of bristles, remainder of unmodified abdominal terga with 2 ½ rows in ♂, 3 in ♀; ventralmost bristle of caudal row below spiracular fossa. Terga 2 5 with 1 apical spinelet on each side. Basal abdominal sternum without setae in ♂, although these often represented by 6–9 microsetae or their bases; in ♀ with about 16–24 small bristles in 2 or 3 highly irregular, oblique or subvertical rows, commencing subdorsally near anterior margin and extending submedially to about ventral ⅙, at caudal ⅓; ventralmost bristles accordingly the most caudal. Representative sterna in ♂ with a caudal row of 3 long subventral bristles, at times surmounted by a small submedian one; with an additional 2 short rows of small subventrals preceding this, plus an anterior 1–2 small ventromarginals making a total of 11–16 in all; in ♀ with about 18–20 bristles in same general pattern but more bristles per row, generally including 5 long bristles in caudal row. Tergum 7 in ♂ with a short dorsal lobe (fig. 165, U.L.7) extending between the sets of antepygidial setae (A.B.); in ♀, both upper lobe (fig 166, U.L.7) and lower lobe (L.L.7) well developed and acute. Three bristles of ♀ 7 T. modified so as to somewhat resemble A.B. and somewhat displaced thereto; uppermost (U.M.B.) at times quite similar to upper A.B., first of lower such (L.M.B.) often contiguous to plate of A.B. and closely resembling upper A.B., generally more so than second (L.M.B.-2). Dorsal A.B. about $\frac{1}{2}$ length of ventral one in ♂; usually slightly longer than $\frac{1}{2}$ in ♀.

Male. Tergum 8 reduced; resembling that of *Medwayella.* Sternum 8 relatively unmodified, lacking a group of close-set bristles or spiniforms; very large, enclosing most of genitalia; extending dorsad to base of anal segments and cephalad to level of base of A.B.; about 1·4 times as long (near ventral margin) as high at maximum level (at cephalodorsal angle). Dorsal margin of 8 T. fairly straight to caudal $\frac{1}{4}$ or beyond; and in some species horizontal; in others, oblique at about angle of 30°; ventral margin varying inversely regarding slope so that narrowing effect is the same, viz., caudal margin about $\frac{1}{2}$ height of cephalic. Manubrium (fig. 165, MB.) broad all the way to near apex; ventral margin biconvex near middle; with a short dorsal distal tubercle. Immovable process of clasper (P.) broadly rounded apically. Conical process (C.P.) fairly broad, at times about 5 times as tall as broad at middle; but in some taxa only about 3 times. Movable finger (F.) very long and thin, about 6·5–7 times as long (from apex of P.) as broad near base of distal fringe (D.FR.), narrowed for most its length; apical margin quite flat. Stiva (STV.) fairly long and narrow. Distal fringe (D.FR.) of about 6–8 bristles commencing on shaft of F. and proceeding onto STV. Sensilla-group (S.G.) consisting of 3 short bristles. Fulcral sclerite (F.S.) higher (longer) than broad; subvertical; broadest at dorsal end; narrowest subventrally. Proximal arm of sternum 9 subvertical; with basal $\frac{2}{3}$ at angle of about 60°; uppermost nearly perpendicular; upper $\frac{1}{3}$ of caudal margin biconcave. Distal ("horizontal" or "ventral") arm of sternum 9 (figs. 167–169, D.A. 9) broad; angled caudad dorsally by virtue of a large mesal flap or extension, the apicocaudal flap (AC.F.9) which is fringed with subspiniforms; apex or subapical region of straight upright portion lobate (A.LB.9) and clothed with thin marginal bristles; with a short apical or subapical, anterodirected spur. D.A.9 apparently with ventral margins fused to about apical third at level of marginal transverse sclerotization (T.S.).

Aedeagal apodeme resembling manubrium for most its length, though broader at apex and lacking an apical tubercle or spur. Its middle lamina (figs 170, 174, M.LAM.) about 3·3–3·6 times as long (to near anterior end of crescent sclerite (C.S.)), or caudal margin of lateral shafts of capsule (L.S.C.) as broad at anterior margin of its bay (B.M.L.). Lateral laminae (L.LAM.) lightly tanned and most noticeable at anterior end, where each extends ventrad of M.LAM.; with ventrocaudad extensions arising from dorsum, near anterior end of B.M.L., and crossing bay but scarcely discernible until underlying proximal arm of sternum 9 (P.A.9), and here appearing as a well tanned line (blending with extensions of girdle (G.) of wall of aedeagal pouch) which continues across M.LAM. to base of Y-sclerite (Y.S.), where it meets the virtually inapparent ventral margin. Ventral wall of aedeagal pouch (AE.P.-V.) well sclerotized, extending to base of body of crochet (B.CR.). Median dorsal lobe (M.D.L.) evenly curved; gradually arching dorsad from level of base of sclerotized inner tube (S.I.T.); height of convexity near level of base of Ford's sclerite (F.SC.) and here only slightly arched. Hood (HD.) relatively tall (long) and narrow; its ventral margin continuing cephalad as the deltoid flap (DEL.FL.) to about level of middle of B.CR.; here DEL.FL. curving dorsad (at times recurving dorsocaudad) to level of pivotal ridge (PIV.R.), in line with base of phylax (PHY.). Anterodorsal angle of DEL.FL. not highly acuminate. Lateral lobes greatly reduced; inapparent. Sclerotized inner tube (S.I.T.) generally so greatly elongated as to be vermiform; apical $\frac{2}{3}$ or $\frac{1}{2}$ arched to form a semi-ellipse; at least 7–12 times as long as broad at middle, and a minimum of 5 times as long as broad at base of phylax; usually 11 times as long as broad at phylax and in some instances, more than 20 times as long as broad. S.I.T. characterized by a sclerite which arises ventrally near its base and loops around the sides of the tube, and which is herein termed lateral wings of ventral armature (L.W.AR.). S.I.T. with a short protrusion from apex (figs 170, 171, FIS.) equivalent to girth of lumen of S.I.T. and dorsally somewhat tanned, appearing as if an extension of a tube within a tube and regarded as comparable to the "fistula" (Peus, 1956), or "outer part of inner tube" (Holland, 1955) or "band of inner tube" (Traub, 1950) associated with ceratophyllids, etc., although much shorter in *Stivalius*. Ford's sclerite (F.SC.) massive, the largest structure in the endchamber; usually flask-shaped or at least constricted subapically; with 1 or 2 claw-like apices (in lateral aspect); not differentiated into securifer and alpha-portions. Phylax (PHY.) well developed as a large sigmoid or bowed sclerite crossing over S.I.T. near base and extending to level of lightly tanned pivotal ridge (PIV.R.), but well anterior to base of F.SC. Pivotal chord (PIV.CD.) feebly sclerotized. Crochet notable in virtually complete reduction of ventral arm, and hence lacking a crochet-process or paramere-like structure. Body of crochet (B.CR.), the upright arm of crochet of other related taxa, well represented, however; relatively long and narrow; base extending from ventral portion of endchamber; apex flattened and expanded, at base of F.SC.; at times (e.g., *S. phoberus*) with a ventral, short, caudad-directed spur, probably representing a vestige of crochet-process. Crescent sclerite (C.S.) large; apex within base of S.I.T. and hence satellite sclerite (SAT.S.) wholly within. Fulcral lateroventral lobes (FUL.L.L.) short. Central sclerite (CEN.S.) appressed to fulcral medial lobes (FUL.M.L.). Lateral shafts of capsule (L.S.C.) well tanned. Y-sclerite (Y.S.) very large; both components visible in mounted specimens. Vesicle (V.) and ventral virga (V.V.) well developed. Penis rods short, scarcely reaching anterior end of apodeme when *in situ*. Third apodemal rod (AP.R.) of endophallus and dorsal virga (D.V.) lightly tanned, especially the latter. Caverna spiculosa (CAV.SPIC.) submedian in position and anterior to level of fulcrum.

Female. Spermatheca (figs 176, SP., 163, 177) with bulga (B.) longer than hilla (H.); bulga broader (taller) caudally than anteriorly and at times constricted in middle; hilla with an apical papilla and somewhat inserted into lumen of bulga. Duct of spermatheca (figs 163, 176–179, D.SP.) with internal striae in dilated portion (DIL.P.) near junction with bursa copulatrix (B.C.), which in turn is thick-walled, very broad most of its length, and generally (fig. 163) markedly involute, or at least coiled or folded upon itself (fig 162), apically, if not elsewhere as well. B.C. with perula not clearly differentiated; with part of inner wall of lumen at times well sclerotized and appearing like a curved band. Wall of roof of oviduct (fig. 163, OV.) well tanned as it (or paired members thereof) approaches vagina (VAG.). Paragenital morion reduced, inapparent; apparently represented by indiscrete lines on each side of B.C., near vagina. Sternum 7 (fig. 175, 7 S.) with ventral ½ of caudal margin biconcave, but upper sinus at times quite small (as in figure). Ventral anal lobe (fig. 176, V.A.L.) with base short; apical margin long; anterior ⅓ of margin somewhat convex and bearing 4–5 close-set, long bristles; remainder of margin sinuate, bearing 2 long bristles at apical ⅓ or ¼. Anal stylet (A.S.) long and narrow, parallel-sided and lacking long subapical bristles. Mesal genitalic ridge of tergum 8 undeveloped. Tergum 8 (8 T.) with a short lobe at ventrocaudal angle. Spiracular fossa 8 (fig. 166, 8 SPC.) medium-sized; upright portion ovate, not much longer than broad. Sternum 8 (8 S.) flask-shaped and with short apical bristles.

COMMENT. Species included: (1) *S. ahalae* (Rothschild, 1904), the type of the genus; from rats, south India; (2) *S. aporus* Jordan & Rothschild, 1922, from *Rattus*, *Millardia* and other murines from Ceylon, India and Nepal. (A subspecies of *aporus*, or a closely related new species, occurs in Thailand and Vietnam on rats.) (3) *S. phoberus* Jordan & Rothschild, 1922, from rats in Ceylon. (4) *S. c. cognatus* Jordan & Rothschild, 1922, *from Rattus* (*Rattus*) in Java; *S. c. spiramus* Jordan, 1926 (new status), from *R.* (*Rattus*) in the mountains of Luzon, Philippines, and the new subspecies next described, from *R.* (*Rattus*) in the mountains of Mindanao, Philippines. (5) *S. rectodigitus* Li & Wang, 1958. Even though the authors state this is near *S. klossi* Jordan & Rothschild, 1922, and compared it with that species, it definitely is close to *S. aporus* (and may be a subspecies thereof) and hence is a member of *Stivalius s. str.*, while *S. klossi* belongs to a separate and yet un-named genus. The status of *S. rectodigitus* is clear, as indicated by Li & Wang's figures of the bursa copulatrix and of the distal arm of the ninth sternum, etc. Further, those authors point out the aedeagal similarities with *S. aporus*.

Further discussion of the genus is presented after the treatment of *S. cognatus* below.

1. ***Stivalius cognatus*** Jordan & Rothschild, 1922

Stivalius cognatus Jordan & Rothschild, 1922. Ectoparasites I : 253, 264, figs 243, 245; Jordan, 1933, Novit. zool. 38 : 355; Costa Lima & Hathaway, 1946, Pulgas: 326; Traub, 1951, Proc. biol. Soc. Wash. 64: 13; Smit, 1958, Bull. Brit. Mus. (Nat. Hist.) Ent. 2(2): 41.

DIAGNOSIS. Immovable process (fig. 165, P.) very short and broadly rounded at apex; with a small subapical caudomarginal bristle. Movable finger (F.) with portion above apex of P. about 6·3 times as long as broad at level of ventralmost bristles of distal fringe (D.FR.); slightly narrowed near basal portion of D.FR., otherwise margins quite straight and parallel; apex subtruncate. Stiva (STV.) of F. well developed; longer than unexpanded portion of apex and about 2·7 times as long as broad. Sclerotized inner tube (figs 170, 173, S.I.T.) elongated, but not nearly as long as in *S. ahalae* and *S. aporus*, i.e., extending only slightly beyond apex of F.SC., instead of for more than ¼ its length; with its arc paralleling that of median dorsal lobe (M.D.L.) instead of being much more complex. Ford's sclerite (F.SC.) narrowed near middle of sclerite, flask-like; with basal portion (proximad of dorsal spur or peak) subequal to portion distad, instead of being ⅔ length of neck of flask. Basal portion of F.SC. only 1·7 times as long as broad at level of dorsal spur instead of 3·5 times. Distal arm of sternum 9 (figs 167–169, D.A.9) with only one spur on anterior (dorsal) margin, occurring at base of apical rounded lobe (A.LB.9), which in turn is not as high as long, instead of vice versa. Sinus above ventral lobe of ♀ sternum 7 (figs 163, 176, 7 S.) somewhat similar in size and shape to that of lobe below it. Bursa copulatrix (figs 163, 177) with convolute portion quite symmetrical in size and shape. Spermatheca (fig. 176, SP.) with bulga (fig. 177, B.) somewhat constricted near middle; caudal ½ more convex dorsally than cephalic portion; slightly more than twice as long as high immediately anterior to constriction (maximum internal measurements); caudal and ventral margins externally quite straight, only slightly convex. Hilla (H.) with about basal ⅕ inserted in lumen of bulga; somewhat squarely recurved at midpoint and slightly dilated above this curve; about thrice as long as broad near bulge; apex broadly rounded. Apical papilla (PAP.) about ⅓-½ diameter of H.; somewhat longer than broad.

For further details of aedeagus, see section 1.c. below, on new subspecies.

COMMENTS. *S. cognatus*, like other members of the genus (*s. str.*), is a typical parasite of members of the subgenus *Rattus*. The original description was based upon material from Java, but Traub (1951) quoted Karl Jordan, F.R.S., as expressing the belief (in litt.) that *S. spiramus* Jordan, 1926, from Luzon, known only in the female, was the same species. Jordan's perspicacity was demonstrated when the writer collected topotypic material of *S. spiramus* in 1961 and found that the specimens were indeed *cognatus*, but of subspecific rank. This subspecies is described below, along with a new one from Mindanao. Undoubtedly other subspecies, and perhaps related species, occur elsewhere in the Indonesian and Philippine Archipelagoes, and our understanding of zoogeography would be enhanced if such material became available for study.

1. a. ***Stivalius cognatus cognatus*** Jordan & Rothschild, 1922

DIAGNOSIS. Characterized by the following features: (1) Distal arm of sternum 9 (fig. 168, D.A.9) with apical lobe (A.LB.9) about 2·4 times as long as high. (2) Apicocaudal flap (AC.F.9) of D.A.9 about 1·6 times as long (from level of margin of transverse sclerotization, T.S.) as broad at middle. (3) Phylax of aedeagus fairly straight and narrow, about 5 times as long as broad at maximum (at middle); scarcely broader at middle than subapically. (4) Ford's sclerite with total length 1·9 times length of basal section (portion anterior to dorsal angle or nubbin) and about 2·5 times breadth at apex of basal section. (5) Bursa copulatrix (fig. 179, B.C.) with coil oblate, rather flattened dorsally. (6) Vertical diameter of involute portion exceeding distance from bottom of loop to vagina (VAG.). (7) Lateral metanotal area usually longer than high (internal measurements).

COMMENT. The only published records for the nominate form are those in the original description, viz., from *Rattus* (*R.*) *rattus* (cited as *Epimys rattus*), from Malang, Java. The specimens studied and the female here illustrated, are from an unrecorded area in Java, coll. M. V. Kuhlavain, and determined by the late Karl Jordan, F.R.S., and received through his kind offices.

ILLUSTRATIONS

168. Distal arm of sternum 9
179. Spermatheca and bursa copulatrix

I. b. ***Stivalius cognatus spiramus*** Jordan, 1926, NEW COMBINATION

Stivalius spiramus Jordan, 1926. Novit. zool. 33 : 391, fig. 12; Costa Lima & Hathaway, 1946, Pulgas: 327; Traub, 1951, Proc. biol. Soc. Wash. 64 : 13.

DIAGNOSIS. (1) Distal arm of sternum 9 (fig. 169, D.A.9) with apical lobe (A.LB.9) about twice as long as high. (2) Apicocaudal flap (AC.F.9) about 1·7 times as long as broad at middle. (3) Phylax (fig. 173, PHY.) symmetrically sigmoid, narrow; about 5 times as long as broad at maximum near middle. (4) Ford's sclerite (F.SC.) 1·6 times as long as its basal portion and 1·9 times as long as broad at apex of proximal region. (5) Bursa copulatrix (fig. 178, B.C.) with involute portion quite circular in outline. (6) Vertical diameter of loop exceeding distance from bottom of coil to level of vagina (VAG.). (7) Lateral metanotal area usually longer than high (internal measurements).

COMMENT. *S. spiramus* was described from, and heretofore known only from, a single female collected by Professor E. H. Taylor at Baguio Bengue (Luzon) from a rat cited by Jordan as "*Rattus guereci.*" (This name probably was a *lapsus* for *querceti* Hollister, 1911, a Luzon rat which is placed by Ellerman (1941) in the *Rattus* (*R.*) *concolor* group but which is treated by Schwarz & Schwarz (1967) as a synonym of *Rattus rattus negrinus* Thomas, 1898.) The present description and figures are based upon specimens which I collected at Baguio, at 3600-4500 ft elev. in October, 1961, ex *Rattus* (*R.*) *rattus* ssp., and which can be considered as topotypic. The allotype ♂ is therefore selected as follows: Allotype ♂ (B-55028) ex *Rattus exulans*; PHILIPPINES: Luzon, Baquio; elev. 3600 ft; 24.X.1961; Coll. R. Traub; deposited in the U.S. National Museum.

ILLUSTRATIONS

169. Distal arm of sternum 9
173. Apical region of aedeagus
175. Sternum 7 (♀)
178. Bursa copulatrix

I. c. ***Stivalius cognatus bamus*** subsp. nov.

TYPE MATERIAL. Holotype ♂, allotype ♀ (B-56383) ex *Rattus rattus mindanensis*; PHILIPPINES: Mindanao, Zamboanga del Norte, Mt Malindang, Masawan, Mutia; elev. 4500–5000 ft; 29.XII.1962; Coll. D.S. Rabor. Paratypes as follows: Collected by D. S. Rabor, 24.XII.1962/14–16.I.1963; same locality as holotype; 27 ♂, 36 ♀ ex *Rattus rattus mindanensis*; 2 ♀ ex *R. rabori*; 2 ♀ ex *R. exulans todayensis*; 1 ♂, 1 ♀ ex *R. pantarensis*; 4 ♂, 4 ♀ ex *Apomys insignis bardus*; 1 ♂, 1 ♀ ex *Rattus* sp., Ibid. but elev. 5200–7000 ft; 2 ♂, 3 ♀ ex *R. r. mindanensis*; Mt Malindang, Canon, Mutia; elev. 3200 ft; 22–24.XII.1961.

Holotype (U.S.N.M. number 71610), allotype and 3 pairs of paratypes deposited in the U.S. National Museum. The remainder distributed as for *M. dryadosa*.

DIAGNOSIS. (1) Distal arm of male sternum 9 (fig. 167, D.A.9) with apical lobe (A.LB.9) about 2·6 times as long as broad. (2) Apicocaudal flap (AC.F.9) relatively short and broad, viz., about 1·3 times as long (from level of caudal margin of transverse sclerotization, T.S.) as broad at middle. (3) Phylax (figs 170, 174, PHY.) eccentrically sigmoid; upper ½ narrower than lower ½ and much more curved; relatively broad, i.e., only 3·4 times as long as broad at maximum breadth (below middle). (4) Ford's sclerite (F.SC.) with basal portion (to level of dorsal nubbin) only ½ total length of F.SC. and about 2·6 times breadth of sclerite at level of dorsal peak. (5) Bursa copulatrix (figs 163, 176, 177, B.C.) with upper portion evenly involute; symmetrical. (6) B.C. relatively long, so that vertical diameter of loop is merely equal in length to lower portion of bursa, i.e., from ventral margin of coil to vagina (VAG.), instead of exceeding it. (7) Lateral metanotal area higher than long (internal measurements).

DESCRIPTIVE NOTES. Since the aedeagus of this species has never been described before, further notes are included here, including comments on this organ as seen from the ventral aspect. It should be borne in mind, however, that most of the points (save for those cited in the diagnosis) are on the species level.

Aedeagus—Lateral Aspect (figs 170, 174). Aedeagal apodeme with middle lamina (M.LAM.) about 3·6 times as long (to level of caudal margin of lateral shafts of capsule (L.S.C.) as broad at anterior margin of its bay (B.M.L.). Hood (HD.) with ventral margin shallowly concave save for curves at anterior and posterior margins; lightly reticulated apically; apparently laterally reinforced by transverse parallel light striae, especially over caudal ⅓, which is the deltoid flap (DEL.FL.). HD. and DEL.FL. extending caudad to base of phylax (PHY.) and body of crochet (B.CR.). Median dorsal lobe sloping at about angle of 30° commencing at level of slightly acute anterodorsal angle of DEL.FL.; maximum height of its gentle, broad arc is at level somewhat apicad of Ford's sclerite (F.SC.) and thereafter sweep of curve paralleling that of dorsal margin of F.SC. (if not pivoted out of position). Aedeagal pouch (AE.P.) with ventral border well tanned; but anterior wall (girdle, G.) less so, and with its cephalodorsad extensions soon meeting the ventrocaudal prolongations of lateral laminae (L.LAM.). Ford's sclerite (F.SC.) with length almost equal to that of body of crochet (B.CR.) and quite broad for proximal ½, which resembles base of a flask; basal ½ with dorsal and ventral margins fairly straight and parallel; narrowed portion of flask slightly more than ½ length; lower margin sinuate. F.SC. with breadth of middle region of anterior ½ equal to that of basal part of sclerotized inner tube

(S.I.T.); apex oblique and subtruncate, terminating in a ventrocaudal projection. S.I.T. with apical ⅔ curved in arc almost paralleling that of M.D.L. but extending more distad, to a level slightly beyond apex of F.SC.; approximate breadth of middle of tube slightly more than ⅗ of that of subapical region of F.SC.; about 10–14 times as long as broad at level immediately proximad of B.CR. Lateral wings of ventral armature (L.W.AR.) somewhat ovate, but narrower dorsally than ventrally and reaching to near dorsal margin of S.I.T. Crescent sclerite fairly long; with a pre-apical anterior hump; narrowed caudally and with caudal ⅓ penetrating S.I.T. where it is virtually contiguous with angled, relatively long satellite sclerite (SAT.S.). Central sclerite (CEN.S.) closely appressed to fulcral medial lobes (FUL.M.L.) and resembling acute wing of an arrowhead. Y-sclerite (Y.S.) with one fork narrow, horizontal and extending to level of base of SAT.S.; larger fork very conspicuous as a diamond-shaped sclerite below fulcrum. Dorsal virga (D.V.) indistinct. Phylax (PHY.) a fairly broad, bowed sclerite which is upcurved below midpoint and somewhat narrowing apically, about 2·3 times as long as broad at maximum girth (below middle) (distinctly narrower in other subspecies). Body of crochet (B.CR.) ribbon-like except for flattened, expanded apex; axis flattened except for somewhat concave extremities; ventrally projecting somewhat below S.I.T. as a narrowed, acute rod, this portion presumably representing a vestige of the crochet-process (paramere) of other genera. Lacking discernible tanned lateral connections between AE.P. and B.CR., with what is apparently a small seta on apical margin of AE.P., on each side, at base of B.CR. and of PHY. With the upper penis rod (P.R.) extending to near level of anterior end of aedeagal apodeme when *in situ*; lower rod much shorter. Ventral virga stout; sclerotized for entire length, viz., to near level of base of bay of middle lamina. Third apodemal rod (AP.R.) lightly tanned once leaving AE.P. Caverna spiculosa (CAV.SPIC.) irregularly ovoid; about twice as long as broad; sloping cephaloventrad at an angle of about 60°.

Aedeagus—Ventral Aspect (fig. 171). Hood with anterior margin entire, lightly tanned. Ford's sclerite shaped like a tulip flower, about 1·3 times as long as broad near base; without any caudad-directed paramere-like structures; the hook-like apex of the lateral aspect actually representing a deep structure extending all the way across the sclerite which is seen on edge. Deltoid flap (DEL.FL.) covering only sides of ventral margin. Phylax (PHY.) actually with base (ventral) fairly narrow and constricted; straddling S.I.T. and apices meeting dorsally above it; therefore projection of PHY. in ventral aspect is that of a trapezoid with thickened sides. Body of crochet (B.CR.) dorsally buttressed against base of F.SC. S.I.T. appearing as a long, narrow cylinder whose only modifications are an apex that is slightly recurved ventrad, viz., the fistula (FIS.), and a narrow, basal belt, viz., the lateral wings of the armature (L.W.A.R). Wall of aedeagal pouch well tanned both laterally (AE.P.-L.) and ventrally (AE.P.-V.); lacking sclerotized connections with body of crochet (unlike the condition in pygiopsyllids with ventral crochet-processes). Vesicle (V.) quite large, and ventral virga (V.V.) broad. Y-sclerite (Y.S.) with bifid anterior base and broad caudal stem flooring middle of capsule, which is quite broad, distance between fulcral lateroventral lobes (FUL.L.L.) nearly equal to length of fulcral area. Caverna spiculosa (CAV.SPIC.) lateral in position.

COMMENT. (1) The vast majority of records of *S. c. bamus* are from *Rattus rattus mindanensis*, with a few from the related murine *Apomys*, all from Mt Malindang at elevations between 3200–5000 ft. As yet material from other parts of Mindanao is unavailable for study, so that the true range of the subspecies is unknown, and also it cannot be stated that this is the only subspecies of *S. cognatus* occurring on the island.

(2) *The aedeagus of S. cognatus.* The structure of the aedeagus as seen in the ventral aspect emphasizes and clarifies some of the points made above, in the consideration of the genus. Thus, the lack of overt connections between the walls of the aedeagal pouch and the crochet is quite striking and is in marked contrast to related taxa. The difference seems to be associated with the presence of a well developed quasi-crochet or ventral crochet-process: if these are present, as in *Medwayella* and *Lentistivalius*, there are definite links between the crochet and the pouch wall; if absent, as in *Stivalius s. str.*, there are no discernible ties. It also is apparent that Ford's sclerite does not bear a pair of narrow hooks or prongs, as one might infer from the lateral aspect. Instead, the apex bears a downward directed flange or lip which extends from one side to the other, and which presumably acts like a prying lever when F.SC. is pivoted ventrad.

Bristles or bristle-like structures are virtually unknown on the aedeagus, and the few isolated examples known to me were regarded as atavisms or freaks. However, the fine seta on each side near the caudoventral margin of the pouch wall in *S. cognatus* can be seen in most specimens and even seems to arise from an alveolus. Since many of the components of the phallosome of fleas are paired, it seems logical to assume the organ is derived from an ancestral bilaterally symmetrical structure, and that this had borne bristles. If so, a setal vestige is not surprising and is in accord with my belief that pygiopsyllids are in general primitive fleas despite certain adaptive specializations, which at times are quite marked.

(3) Abnormal structures of fleas are often of interest in that they may represent atavisms or anomalies that suggest the origin of the normal organ. A freak bristle is therefore labelled FRK. in fig. 165, although no further comments can be made at this time on its possible significance.

ILLUSTRATIONS

163. Spermatheca and genitalia (♀)
164. Head and prothorax (♂)
165. Processes of clasper
166. Antepygidial region (♀)
167. Distal arm of sternum 9
170. Apical region of aedeagus (lateral)
171. Apical region of aedeagus (ventral)
174. Apical region of aedeagus
176. Spermatheca, genitalia and anal segments
177. Spermatheca and bursa copulatrix

2. COMMENTS ON ***Stivalius*** *s. str.*

Host-Relationships, Distribution and Potential Vectorship of Disease.

Throughout its known range (Ceylon, Indian Subcontinent, S.E. Asia, Indonesia and the Philippines) the genus *Stivalius s. str.* is primarily associated with murine rodents, especially the subgenus *Rattus*. Blood-sucking ectoparasites of murines are of special interest regarding transmission of disease, but the role of *Stivalius s. str.*

in this regard is in need of clarification. *Stivalius cognatus*, reported as *Pygiopsylla ahalae* in Java according to Pollitzer & Meyer (1961), and, *Stivalius* species "have been found capable of transmitting plague in Java and south India" respectively (Pollitzer, 1954). Inasmuch as the studies referred to by Pollitzer concern *Stivalius* from rats, the species in question are almost undoubtedly members of *Stivalius s.str.*, e.g., *S. ahalae*, *S. cognatus* and *S. aporus* (or *S. phoberus*, if it occurs on the mainland and not merely Ceylon), since the only other Indian "*Stivalius*" is the species referred to above, in the present paper, as *Lentistivalius ferinus*, and is a parasite of shrews. The role of *Stivalius* in the ecology of both human and murine plague needs elaboration especially since this disease is still endemic in areas where plague exists today in Indonesia, Thailand and Vietnam and where members of this genus are known to, or may be expected to infest *Rattus* (*Rattus*). The possible involvement of *Stivalius s. str.* in the ecology of murine typhus should be investigated, for this flea-borne disease is likewise associated with the subgenus *Rattus* and is endemic, or presumed to occur, in regions where *Stivalius s. str.* infests commensal rats.

The Specialized Aedeagus and Bursa Copulatrix

Stivalius s. str. exhibits some remarkable genitalic modifications that are not seen in related taxa, many of which have developed other complexities in the sexual apparatus. The marked elongation of the sclerotized inner tube (figs 170–171, 173–174, S.I.T.) is quite striking as compared to *Lentistivalius*, for example (fig. 172). Moreover, the apex of S.I.T. is further specialized in *Stivalius s. str.* by the apically protruding, somewhat tanned fistula (fig. 170, FIS.). There are scores of species referable to *Stivalius s. lat.*, and it can be no coincidence that females in which the bursa copulatrix is broad, sausage-like and coiled (and no others) are the mates of males with snake-like aedeagal tubes. Such parallel developments in the two sexes of *Stivalius s. str.* in the course of evolution strongly suggest a functional and fundamental relationship, namely that, in this taxon, unlike the case in most fleas, S.I.T. itself, and not merely the penis rods,[15] enters well into the bursa. This then would explain the thickened walls of the bursa and the sclerotized rod-like lining of one side of the lumen of the bursal duct seen in this genus.

Two points are mentioned here as rendering support to this hypothesis. The characteristic absence of ventral "parameres" in *Stivalius s. str.* indicates that the function of the caudad-directed, finger-like or rectangular crochet-process (CR.P.) of related taxa has been taken over by some other structure. The crochets of ceratophyllids, leptopsyllids and some other fleas serve to secure and maintain a hold on the female genitalic apparatus and to open some of the components to the male organs (Holland, 1955, Goncharov, 1964). Presumably the unusually well developed Ford's sclerite (F.SC.) of *Stivalius s. str.* assumes some of these functions in the absence of the crochet-process, as is suggested by the hook-like appearance of its apex (fig. 170), which, as can be seen in ventral aspect (fig 171) is really a down-projecting flange and which presumably acts as a pry when the apex of F.SC. is tilted ventrad. It also seems logical to believe that the hypertrophied and specialized S.I.T. takes over other functions, especially since there are instances within the Order wherein the aedeagal tube apparently is the true penetrating copulatory organ, and not the penis rods. Thus, Barnes and Radovsky (1969) cite impressive morphological evidence for this belief, in the case of *Tunga* Jarocki, 1838, and Suter's figures (1964) of copulating *Tunga* seem to bear this out. The second point suggesting that these modifications in the male and female of *Stivalius s. str.* are correlated, is the illustrative case of *S. phoberus* Jordan & Rothschild, 1922. Here S.I.T. is not as narrowed and elongated as in other species of the taxon, i.e., it is only 5 times as long as broad at level of phylax, instead of 9–20 times. In this species (fig. 162) the bursa is not as modified either: it is less involute and not quite as broad throughout (*cf.* fig. 163, *S. cognatus bamus*).

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[15] Holland (1955) reiterated the view of Snodgrass (1946) that the penis rods ". . . are the only elements of the intromittant apparatus that are capable of being protracted from the aedeagus . . ." When Holland (p. 245) speaks of the "long outer part of the aedeagal inner tube" (not to be confused with sclerotized inner tube) as being "inserted well within the bursa copulatrix," and other writers make similar statements, they are referring to a structure that is regarded as already being *outside* of S.I.T. Thus, there is no contradiction, for the outer tube is not being protracted from S.I.T. This outer tube is the structure referred to above as the fistula (FIS.).

Moreover, it should be borne in mind that Snodgrass, Traub (1950), Holland, Goncharov (1964 a & b) and others, when discussing the copulatory apparatus or copulation in Siphonaptera, were referring to specific taxa of fleas and their observations do not necessarily apply to other fleas. Pygiopsyllids and rhopalopsyllids in particular have not been studied in this regard.

In *Medwayella* and *Lentistivalius*, which possess well developed caudad-directed ventral crochet-processes, there are obvious tanned connections between the wall of the aedeagal pouch and the crochets. It is noteworthy that in *Stivalius s. str.*, which lack ventral "parameres" and crochet-processes, such bonds are inapparent, even in the ventral aspect (fig. 171), as is pointed out below.

A test of this hypothesis may be provided by another group of pygiopsyllid fleas in which the basal half of the bursa copulatrix is very broad and thickened, namely the three species of *Acanthopsylla* Jordan & Rothschild, 1922, in which there is but 1 (not 2 or 4) spiniforms on the frontal region of the head, viz. *A. praxilla* M. Rothschild, 1934, *A. guba* Smit, 1953 and *A. richardsoni* Smit, 1953. In the other members of the genus (which includes a total of 16 species), the ventral portion of the bursa is not conspicuously dilated and lacks ring-like striations. In these 13 other species, the sclerotized inner tube of the aedeagus is not elongate, corresponding to the relative size typical for the bulk of the pygiopsyllids. In the *A. praxilla*- group the male is known only for one species (*A. richardsoni*), which I have not seen, and its aedeagus has never been figured. However, the shape of the bursa copulatrix in this group of fleas is so suggestive of the condition in *Stivalius s. str.* that I expect that here too the sclerotized inner tube of the male must be elongate, if not ophidian in shape, and that ventral crochet- like processes are lacking.

Evolutionary Status of STIVALIUS S. STR.

It is noteworthy that this taxon, which is the most highly specialized of this group of pygiopsyllids with respect to modifications of the aedeagus and the co-functional bursa copulatrix, consists of characteristic parasites of the subgenus *Rattus*, the most modern and highly developed of the murines. This suggests that *Stivalius s. str.* is likewise at the pinnacle of the evolutionary development of this complex of genera to date. These points are discussed further in the two following articles in the series.

3. KEY[16] TO THE KNOWN SPECIES AND SUBSPECIES OF **STIVALIUS** JORDAN & ROTHSCHILD, 1922, *s. str.*

1 Male with scolerotized inner tube of aedeagus (figs 170, 173, S.I.T.) at least 9 or more times as long (from base) as broad at base of phylax (PHY.) and 20–30 times as long as broad at middle. Female with bursa copulatrix (figs 163, 178, B.C.) markedly involute, the coil(s) quite symmetrical and not overlying vertical (ventral) portion of tube; often large, involving most of length of bursa. (Indian Subcontinent to Philippines) 2

Sclerotized inner tube only about 5 times as long as broad at base of phylax and about 9 times as long as broad at middle. Bursa copulatrix (fig. 162, B.C.) folded upon itself at upper ⅓, the loop asymmetrical. (Ceylon) . . ***phoberus*** J. & R., 1922

2 Arc of S.I.T. (figs 170, 173) shallow, equivalent to curve of median dorsal lobe (M.D.L.), extending only slightly beyond apex of Ford's sclerite (F.SC.), i.e., only for a distance equivalent to less than ⅕ its total length. Basal portion of F.SC., i.e., region proximad to subapical constriction and below nubbin (peak or spur) on dorsal margin, equals about ½ length of F.SC.; this section only 1·7 times (or less) as long as broad at level of spur. Distal arm of sternum 9 (figs 167–169, D.A.9) with only one spur on anterior (dorsal margin, and that at base of apical rounded lobe (A.LB.9)). Subventral sinus of ♀ sternum 7 (figs 163, 176, 7 S.) almost an inverted and reversed image of ventral lobe, its dorsal margin continuing caudad to or beyond level of margin of ventral lobe before turning dorsad. Ventral lobe of 7 S. narrower than basal part of sinus above it. (Indonesia and Philippines) ***cognatus*** subsp. 5

– S.I.T. with arc much more convex than M.D.L. and equivalent to ½ a broad ellipse, extending beyond apex of F.SC. by more than ¼ its length. Basal portion of F.SC. at least ¾ length of F.SC. and at least 3·5 times as long as broad at level of nubbin (peak or spur) on dorsal margin. D.A.9 with 2 spurs on anterior (dorsal) margin; the additional one proximad of that at base of apical rounded lobe. Subventral sinus of ♀ 7 S. incomplete, not shaped like ventral lobe due to its dorsal margin being more oblique than ventral one or else sharply curving dorsad near base of sinus. Ventral lobe of 7 S. broader (taller) than basal part of sinus above it. (Indian Subcontinent and Ceylon or Yunnan or Southeastern Asia) 3

3 Dorsolateral bristles of hind-tibia with bristles of groups dissimilar in size, the groups fairly widely separated from one another so that there is no resemblance to a comb. S.I.T. extremely long and narrow, at least 18 times as long as broad at base of phylax. F.SC. with only 1 apical prong. Phylax greatly dilated at middle; both margins here convex; only about 2·4 times as long as broad at middle. ♀ 7 S. with upper angle of dorsal sinus acute and projecting as a short thumb ***ahalae*** (Roths., 1908)

– Dorsolateral bristles of hind-tibia with inner members of groups often similar in size and girth and so arranged that apical ½ of tibia bears a nearly perfect comb. S.I.T. elongate, but not so markedly, about 15 times as long as broad at base of phylax. F.SC. with 2 apical prongs. PHY. with only anterior margin convex at middle; about thrice as long as broad at middle. ♀ 7 S. with upper angle of dorsal (lateral) sinus short, not projecting as a thumb 4

4 Distal portion of F.SC. (apicad of nubbin) relatively broad, only about twice as long as broad. Notch at apex of F.SC. with prongs converging somewhat at tip. Seventh sternum of female with lobe above subventral sinus extending more

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[16] Only one character per couplet need apply, since these are not combinations of characters. Several alternates are cited to ease identification.

caudad than does ventral lobe; this median lobe smaller than ventral lobe. (Yunnan, Indo-China, Thailand) . . . . . **rectodigitus** (Li & Wang, 1958)[17]

– Distal portion of F.SC. narrow, about thrice as long as broad. Notch at bifid apex of F.SC. with prongs diverging at tip or, at most, parallel. Seventh sternum of female with median lobe subequal in size and extent to subventral one (Indian subcontinent and Ceylon) . . . . **aporus** Jordan & Rothschild, 1922

5 PHY. (figs 170, 174) relatively broad, about 2·3 times as long as broad at maximum level. Apicocaudal flap (AC.F.9) of D.A.9 relatively short and broad, viz., length (from level of caudal margin of transverse sclerotization, T.S.) only about 1·3 times breadth at middle. B.C. (fig. 177) relatively long, viz., vertical diameter of involute portion equal to distance from bottom of loop to vagina (VAG.). The portion of wall of B.C. which is anterior to tanned lining of lumen, broader than wall of opposite side of duct. Lateral metanotal area with internal dimensions taller than long at subdorsal level. (Mindanao) **cognatus bamus** subsp. n. (p. 287)

– PHY. (fig. 173) narrow; about 5 times as long as broad at maximum level. AC.F.9 (figs 168, 169) comparatively longer and narrower, at least 1.6 times as long as broad at middle. B.C. (figs 178, 179) with vertical diameter of involute portion exceeding distance from bottom of loop to vagina (VAG.). Portion of wall of B.C. which is anterior to tanned lining of lumen, narrower than opposite wall. Lateral metanotal area generally longer than high (internal measurements). (Java and Luzon) 6

6 F.SC. (fig. 173) proportionately short and broad; total length only about 1·6 times as long as its basal portion (to level of dorsal nubbin) and 1·9 times as long as broad at level of dorsal spur. PHY. symmetrically sigmoid. Apical lobe (fig. 169, A.LB.9) of D.A.9 relatively tall, only twice as long as high. B.C. (fig. 178) with involute portion quite circular in outline. (Luzon) **cognatus spiramus** Jordan, 1926 (p. 287)

– F.SC. relatively long and narrow; about 1·9 times length of its basal portion and about 2·5 times as long as broad at apex of basal section. PHY. quite straight, definitely not sigmoid. A.LB.9 (fig. 168) proportionately short, about 2·4 times as long as high. B.C. (fig. 179) with involute portion oblate, rather flattened dorsally. (Java) . . . . . . **cognatus cognatus** J. & R., 1922 (p. 286)

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[17] *S. rectodigitus* was described from specimens from Yunnan. I have seen only specimens from Thailand, Vietnam and Laos, which closely resemble the figures and description of Li & Wang, but which I had regarded as subspecies of *S. aporus*. Further study, including specimens from Yunnan, are required to clarify the status of *S. rectodigitus*, but I am inclined to consider it a subspecies of *S. aporus*. Also, the key-characters cited above for the separation of the females may prove unreliable, but females of related forms of *Stivalius s. lat.* are often difficult or impossible to identify in the absence of associated males.

North Borneo as members of USAMRU in 1951 or 1953 included Capt. C. L. Wisseman, Jr., M.C.,[18] David H. Johnson, Ph.D. (Smithsonian Institution), Charles Wharton, Capt. H. D. Newson, M.S.C., and Capt. B. C. Walton, M.S.C. Scientists from DMZ-IMR on those or other trips to Borneo (i.e., 1953, at Mt. Trus Madi) included Dr. J. R. Audy and Dr. J. L. Harrison, who also were responsible for the DMZ-IMR collections from 1947 onwards, for 10 or more years. B. L. Elisberg, M.D., H. E. McClure, Ph.D., Lt. V. J. Tipton, M.S.C., participated in the USAMRU studies in Malaya at various times. Integral members of the field-teams in Malaya, N. Borneo and Sarawak (1958) were Ben Ensoll and Phang Ong Wah (USAMRU) and Lim Boo Liat and M. Nadchatram (DMZ-IMR). Yoon Yuen Fat and Ng Cheong Kee served on some of the USAMRU trips in Malaya and the latter worked on Tioman Island with UM. The USAMRU teams were all field-units of the Walter Reed Army Medical Center, Washington, D.C.

The accomplishments of Lord Medway's expedition to Gunong Benom are amply attested throughout this volume, but Lord Medway also helped us obtain valuable specimens from other parts of Malaya and North Borneo as well. Dr. J. A. Bullock (UM) was most helpful in providing fleas from northern Malaya and Tioman Island. The Bernice P. Bishop Muesum, via J. L. Gressitt, Ph.D., sent for study, specimens from Java collected by J. M. Stusak. R. E. Elbel, who served with Dr. Audy in N. Borneo in 1953, also collected the bulk of the Thai specimens, while with the U.S. Operational Mission to Thailand. Additional Thai material was provided by Lt.Col. J. E. Scanlon, M.S.C., and other members of the U.S. Component of the SEATO Medical Research Unit in Bangkok. Dr. Boonsong Lekagul was extremely helpful during all the studies in Thailand, as was Kitti Thonglongya.

Special thanks are due to Dr. T. C. Maa of the staff of the Bishop Museum for the great efforts he expended, under difficult conditions, in collecting fleas in Indonesia, Sarawak, Malaya, New Guinea and elsewhere, while simultaneously making superb collections of other kinds of insects.

F. G. A. M. Smit of the British Museum (Natural History), rendered great assistance by lending me paratypes and unidentified specimens from the Rothschild Collection of Fleas, thereby providing us with a new species for description, while another new species was received from the Director of the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands. Mr. Smit was also very helpful in determining some of the precise localities in Malaya, Java and Sumatra where specimens in the N. C. Rothschild Collection had been collected.

The illustrations in this series of articles were prepared by members of our Department at Baltimore. Of the photographs 93 are the work of J. Navarro, while Mrs. Suzanne L. Shipley prepared 33 photographs or drawings, including the difficult figures of the dorsal or ventral aspects of the aedeagus. Thirty-three of the illustrations were drawn by Mrs. Avonne Green. The bulk of the figures of *L. vomerus* were prepared by Miss Ermona McGoodwin, but those of the male genitalia are composites made by her and R. Traub. The dissections were prepared by the latter and mounted by Mrs. Phunthong Malikul. Miss Helle Starcke and T. M. Evans rendered considerable editorial assistance.

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[18] The military rank cited in each instance is that borne at the time the work was done.

The mammals were identified by J. L. Harrison and Lim Boo Liat (for Malayan and Bornean mammals), Lord Medway (Malaya), D. H. Johnson (N. Borneo and Thailand), Kitti Thonglongya (Thailand for SEATO) and R. E. Elbel (some Thai hosts). With respect to names of hosts, Lord Medway's book on Bornean mammals was followed (1963), as well as Harrison's works on the Malayan (1966) and Bornean (1964) mammals. The opus by Ellerman and Morrison-Scott (1951) was utilized for palaearctic mammals, as were the volumes by Ellerman (1940, 1941, and 1949) in some other instances. The scheme of classification followed is essentially that of Simpson (1945) and that of Anderson and Jones (1967), but with modification for the classification of higher taxa of New World mammals as per Hershkovitz (1966, 1969). In instances where there was a conflict in generic names, Walker et al. (1964) was followed, because he generally was the latest reviser. A complete list of relevant host names is appended.

My thanks are extended to all of these associates for their cheerful and cheering help.

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LIST OF HOST-NAMES[19]

Apodemus speciosus Temminck, 1845
Apomys Mearns, 1905
Callosciurus Gray, 1867
Callosciurus caniceps (Gray, 1842)
Callosciurus erythraeus (Pallas, 1779)
Callosciurus finlaysoni (Horsfield, 1824)
Callosciurus n. nigrovittatus (Horsfield, 1824)
Callosciurus notatus (Boddaert, 1785)
Callosciurus notatus miniatus (Miller, 1900)
Callosciurus prevosti (Desmarest, 1822)
Dremomys Heude, 1898
Dremomys rufigenis (Blanford, 1878)
Epimys rattus (Linnaeus, 1758)
Hylopetes Thomas, 1908
Iomys horsfieldi (Waterhouse, 1837)
Lariscus Thomas & Wroughton, 1909
Lariscus insignis (Cuvier, 1821)
Menetes berdmorei (Blyth, 1849)
Millardia Thomas, 1911
Petaurista Link, 1795
Petaurista elegans (Müller, 1839)
Ptilocercus lowi (Gray, 1848)
Rattus Fischer, 1803
Rattus (*Lenothrix*) *canus* (Miller, 1903)
Rattus (*Lenothrix*) *rajah* (Thomas, 1894)
Rattus (*Lenothrix*) *surifer* (Miller, 1900)
Rattus (*Leopoldamys*) *sabanus* (Thomas, 1887)
Rattus (*Maxomys*) *cremoriventer* (Miller, 1900)
?*Rattus* (*Maxomys*) *fulvescens temmincki* Kloss, 1921 (for "Rattus bukit temmincki")
Rattus (*Rattus*) Fischer, 1803
Rattus (*Rattus*) *concolor* (Blyth, 1859)
Rattus (*Rattus*) *querceti* Hollister, 1911
Rattus (*Rattus*) *rattus* (Linnaeus, 1758)
Rattus (*Rattus*) *rattus mindanensis* (Mearns, 1905)
Rattus (*Rattus*) *rattus negrinus* Thomas, 1898
Rattus (*Rattus*) *tiomanicus* (Miller, 1900)
Rattus (*Rattus*) *tiomanicus jalorensis* (Bonhote, 1903)
Rattus (*Stenomys*) *bowersi* (Anderson, 1879)
Rattus (*Stenomys*) *muelleri* (Jentink, 1879)
Ratufa Gray, 1867
Rhinosciurus Blyth, 1855
Rhinosciurus laticaudatus (Müller, 1844)
Sundasciurus Moore, 1958
Sundasciurus brookei (Thomas, 1892)
Sundasciurus hippurus (Geoffroy, 1832)
Sundasciurus lowi (Thomas, 1892)
Sundasciurus tenuis (Horsfield, 1824)
Tamiops mcclellandi (Horsfield, 1839)
Tupaia Raffles, 1821
Tupaia glis (Diard, 1820)
Tupaia javanica Horsfield, 1822
Tupaia javanica occidentalis Robinson & Kloss, 1918
Tupaia minor Günther, 1876
Tupaia tana Raffles, 1821

LIST OF LANDMARKS AND POINTS OF REFERENCE

(Figs 1–3, 28 and 29)

FIG. 1

a	Anteroventral angle of tergal apodeme of ♂ segment 9 (T.AP.9).
b	Ventral sinus of T.AP.9.
c	Anterodorsal angle of T.AP.9.
d	Dorsal sinus of T.AP.9 and base of anterior margin of conical process (C.P.).
e	Apex of C.P.
f	Level of middle of C.P.; anterior margin.
g	Level of middle of C.P.; posterior margin.
h	Middle of base of C.P.
i	Point of maximum convexity on anterior margin of movable finger (F.).
j	Level of narrowest subapical portion of F.; anterior margin.
k	Level of narrowest subapical portion of F.; posterior margin.
l	Level for measuring length of dilated portion of apex of F.; anterior margin.
m	Apicodorsal angle of F.
n	Midpoint of apical margin of F.; for measuring height of F.
o	Level of base of stiva (STV.); a projection of posterior margin of F. at narrowest level (k).

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[19] Not all of these names are necessarily regarded by mammalogists as valid today.

p	Apex of stiva.
q	Point of maximum convexity on posterior margin of F.
r	Level of most apical portion of immovable process of clasper (P.).
s	Level of r, projected to longitudinal axis of F.
t	Level of base of bulge at apex of P.
u	Point of maximum convexity on upper or dorsal bulge on posterior margin of manubrium (MB.).
v	Point of maximum concavity on sinus on posterior margin of MB.
w	Point of maximum convexity on lower or apical bulge of MB.
x	Base of apical cap of MB. (posterior margin).
y	Tip of apical cap of MB.
z	Base of apical cap of MB. (anterior margin).
aa	Apex of anterior (ventral) margin of proximal arm of sternum 9 (P.A.9).
bb	Apex of posterior (dorsal) margin of P.A.9.
cc	Subapical bulge (convexity) on anterior margin of P.A.9.
dd	Posterior or ventral bulge on anterior margin of P.A.9.
ee	Point on posterior margin of P.A.9 that is opposite cc (paralleling chord on arc aa–bb).
ff	Point on posterior margin of P.A.9 that is opposite dd.
gg	Lowest point on trough or "U" on dorsal margin at base of P.A. 9.
hh	Point on ventral margin of P.A.9 opposite gg.
ii	Base of distal arm of sternum 9 (D.A.9); anterior margin.
jj	Anterior (dorsal) end of transverse sclerotization (T.S.) of D.A.9 and level of base of ventral (caudal) margin of mid-microspiculate area (M.MSP.).
kk	Base of sclerotized part of apical half of D.A.9; distad of mid-microspiculate area (M.MSP.) and level of proximal-most of caudomedial group of spiniform bristles (CM.G.B.) (see also fig. 3).
ll	Proximal marginal point of base of subapical lobe (SUB.L.), at level of proximal-most bristle of SUB.L.
mm	Apex of SUB.L. (see also fig. 3).
nn	Midpoint of imaginary chord connecting edge of subapical notch (NCH.).
oo	Apicoventral angle of apical lobe AP.L. of D.A.9.
pp	Midpoint on margin of AP.L.
qq	Apicodorsal angle (or point in line with oo) on AP.L. (see also fig. 3).
rr	Lowest point in subapical notch (NCH.) on D.A.9.
ss	Level of distalmost member of subapical group of spiniforms (SG.SPN.).
tt	Level of proximal-most of CM.G.B.
uu	Posterior (ventral) margin of T.S.
vv	Base of D.A.9 (posterior margin).
ww	Anteroventral angle of upper margin of fulcral sclerite (F.S.).
xx	Caudodorsal angle of upper margin of fulcral sclerite (F.C.)
yy	Dorsal extension of F.S. curving to ventrocaudal angle of F.
zz	Anteroventral angle of lower or ventrocaudal margin of F.S.
a3	Upper angle of ventrocaudal margin of F.S., opposite zz.

FIG. 3

b3	Dorsal point of transverse sclerotization (T.S.) of D.A.9 in *M. loncha* and allies (but not ventral margin of M.MSP.).
c3	Ventral or proximal base of spur-like subapical lobe (SUB.L.) of D.A.9 in *M. loncha* and allies.
d3	Thickening at base of SUB.L.
e3	Dorsal or apical base of SUB.L.
f3	Semimembranous margin of D.A.9 distad of e3.
g3	Level of base of spinform opposite d3 at base of SUB.L.

FIGS 28, 29

h3	Dorsal margin of 8 S.—projection of upper portion (anterior fork) of SU.8.
i3	Dorsalmost point of 8 S.
j3	Dorsal margin—in line with middle of dorsal margin (o3) of LUM. and dorsalmost median large bristle (k3).
k3	Dorsalmost large median bristle (in line with middle of LUM.).
l3	Point on anterior margin, near middle, in line with largest caudomarginal bristle (m3).
m3	Longest and secondmost dorsal, caudomarginal bristle.
n3	Anteriormost point on tanned dorsal margin of LUM.
o3	Middle of LUM. as located on dorsal margin.
p3	Ventrocephalad corner of 8 S.
q3	Anteriormost point on ventral margin of LUM. indicated by limit of dense group of rows of spiniforms.
r3	Point on ventral margin directly below highest point (i3).
s3	Caudal apex of LUM.
t3	Ventrocaudal corner of 8 S.

FIG. 3

u3	Projection of axis of T.S. to ventral margin of D.A.9.

FIG. 2

v3	Level of dorsal margin of head at falx.
w3	Falx.
x3	Point along antennal fossa in line with bottom of median sensory crater (M.S.C.).
y3	Point along frons in line with x3.
z3	Point along frons in line with base of uppermost bristle of row I.
a4	Point along antennal fossa in line with z3.
b4	Point along frons in line with base of uppermost bristle of row II.
c4	Point along antennal fossa in line with labral bristles (d4) and base of eye-bristle (E.B.).
d4	Level of labral bristles.
e4	Point along antennal fossa in line with labral bristles and E.B.
f4	Point on ventral margin of gena in line with w3 (falx) and height of convexity of first ventral arc of gena.
g4	Point of height of convexity of second ventral arc of gena.

LIST OF ABBREVIATIONS

A.B.	Antepygidial bristles.
A.G.	Apical group of dorsomarginal bristles on tibia.
A.LB.9	Short apical lobe on D.A.9.
A.S.	Anal stylet.
AC.F.9	Apicocaudal flap of D.A.9.
AE.A.	Aedeagal apodeme.
AE.F.	Aedeagal fulcrum.
AE.P.	Aedeagal pouch.
AE.P.-L.	Lateral walls of AE.P.
AE.P.-V.	Thickened ventral walls of AE.P.
ALPH.	Alpha-portion of Ford's sclerite.
AN.GP.	Anterior group of marginal bristles on F.
AP.L.	Apical lobe of D.A.9.
AP.R.	Third apodemal rod of endophallus.
ARC.	Broad sinus or arc on D.A. 9.
B.	Bulga (head) of spermatheca.
B.C.	Bursa copulatrix.
B.CR.	Body of crochet.
B.M.L.	Bay of middle lamina.
B.MB.	Bay of manubrium.
C.P.	Conical process on anterior portion of P.
C.S.	Crescent sclerite of aedeagus.
CAV.SPIC.	Caverna spiculosa.
CEN.S.	Central sclerite of aedeagus.
CM.G.B.	Caudomarginal group of stout bristles on D.A.9.
COX.1	Procoxa.
COX.3	Metacoxa.
CR.P.	Crochet process.
D.A.L.	Dorsal anal lobe of proctiger.

D.A.9	Distal arm of male sternum 9.
D.B.C.	Duct of bursa copulatrix.
D.FR.	Distal fringe of long bristles on caudal margin of F.
D.S.C.	Dorsal sensillary crater of pre-antennal region.
D.SP.	Duct of spermatheca.
D.V.	Dorsal virga.
D.VG.	Duplicatura vaginalis.
DEL.FL.	Deltoid flap of hood of aedeagus.
DIL.P.	Dilated portion of duct of spermatheca.
DM.1–6	Groups of dorsolateral bristles arising from marginal notches on tibia.
E.B.	Large bristle in front of or near eye.
E.R.B.	Eye-row of bristles.
EXT.9	Spur-like extension of ventral apical margin of D.A.9.
F.	Movable finger or process of clasper.
F.S.	Fulcral sclerite at base of attachment of F.
F.SC.	Ford's sclerite.
FIS.	Fistula.
FM.1	Profemur.
FRK.	Freak—grossly abnormal bristle.
FUL.L.L.	Fulcral lateral lobes of aedeagus.
FUL.M.L.	Fulcral medial lobe of aedeagus.
G.	Girdle of aedeagal pouch.
G.R.B.	Genal row of bristles.
G.VG.	Glandula vaginalis.
GRV.	Groove-like structure of Ford's sclerite.
H.	Hilla (tail) of spermatheca.
HD.	Hood of aedeagus.
HOM.	Homolate margin proximad of apex of D.A.9.
L.A.	Lower arm of securifer.
L.L.	Lateral lobe of aedeagus.
L.L.7	Lower lobe of tergum 7, below plate of antepygidial bristles.
L.LAM.	Lateral laminae of aedeagal apodeme.
L.M.	Lateral metanotal area of metathorax.
L.M.B.	Lower modified bristle(s) of 7 T.
L.M.B.-2	Second or ventral L.M.B.
L.P.	Labial palpus.
L.S.C.	Lateral shafts of capsule of aedeagus.
L.W.AR.	Lateral wings of ventral armature of S.I.T.
LUM.	Lumacaudate process.
M.D.L.	Median dorsal lobe of aedeagus.
M.LAM.	Middle lamina of aedeagal apodeme.
M.MSP.	Mid-microspiculate area of D.A.9.
M.P.	Maxillary palpus.
M.R.8	Mesal tanned genitalic ridge of ♀ 8 T.
M.S.C.	Median sensillary crater of pre-antennal region.
MB.	Manubrium.
MPM.	Mesepimere.
MPS.	Mesepisternum.
MSN.	Mesonotum.
MSP.P.	Patch of microspicules near apex of D.A.9.
MTM.	Metepimere.
MTN.	Metanotum.
MTS.	Metepisternum.
MX.	Maxillary lobe.
NCH.	Subapical notch on anterior margin of D.A.9.
OV.	Oviduct.
P.	Immovable process of clasper.
P.A.9	Proximal arm of ♂ sternum 9.
P.B.C.	Perula—dilated portion of bursa copulatrix.
P.R.	Penis rods.
P.W.EX.	Extension of aedeagal pouch wall.
PAP.	Apical papilla on bulga.
PG.M.	Paragenital morion.
PHY.	Phylax.
PIV.CD.	Pivotal chord linking phylax and Ford's sclerite.
PIV.R.	Pivotal ridge of phylax.
PK.	Peak of bulga.
PL.A.	Pleural arch of metathorax.
PS.S.	Pseudosetae.
Q.C.	Quasi-crochet.
S.G.	Group of sensilla near antero-distal angle of F.
S.G.SPN.	Subapical group of short spiniforms on caudal margin of D.A.9.
S.I.T.	Sclerotized inner tube of aedeagus.
S.LUM.	Apical fold or seam of LUM.
S.S.	Subanal sclerite of male.
SAC.	Large sac associated with perula.
SAT.S.	Satellite sclerite of aedeagus.
SEC.	Securifer—ventrocaudal or apical member of Ford's sclerite.
SN.	Sensilium.

SP.	Spermatheca.
SPIC.L.	Ventral lamella or semimembranous spiculose lobe arising from base of PHY.
SQ.	Squamulum.
STV.	Stiva—caudodistal expansion of F., resembling a plow-handle in shape.
SU.8.	Suture delimiting more heavily sclerotized mesal area of ♂ 8 S.
SUB.L.	Subapical lobe on anterior margin of D.A.9.
SUP.FL.	Supramedial flap of D.A.9.
SUP.G.	Supramedial group of thin bristles on D.A.9.
SY.	"Supernumerary" bristles between rows on head.
T.AP.9	Tergal apodeme of segment 9.
T.L.S.	Tendons of lateral shafts of aedeagus.
T.S.	Transverse submedian sclerotization of D.A.9.
THK.	Sclerotized thickening associated with SUP.FL.
THM.	Thumb-like apex of alpha-portion of F.SC.
U.A.	Upper arm of securifer.
U.L.7	Upper lobe of tergum 7, above plate of antepygidial bristles.
U.M.B.	Upper modified bristle of 7 T.
V.	Vesicle of aedeagus.
V.A.L.	Ventral anal lobe of proctiger.
V.S.C.	Ventral sensillary crater of preantennal region.
V.V.	Ventral virga.
VAG.	Vagina.
VC.1–4	Vinculum 1–4.
Y.S.	Y-sclerite of aedeagus.
1 T.	First tergum.
2 S.	Second sternum.
2 T.	Second tergum.
6 S.	Sixth sternum.
6 T.	Sixth tergum.
7 S.	Seventh sternum.
7 SPC.	Spiracle (fossa) of seventh segment.
7 T.	Seventh tergum.
8 S.	Eighth sternum.
8 SPC.	Spiracle (fossa) of eighth segment.
8 T.	Eighth tergum.
9 S.	Ninth sternum.

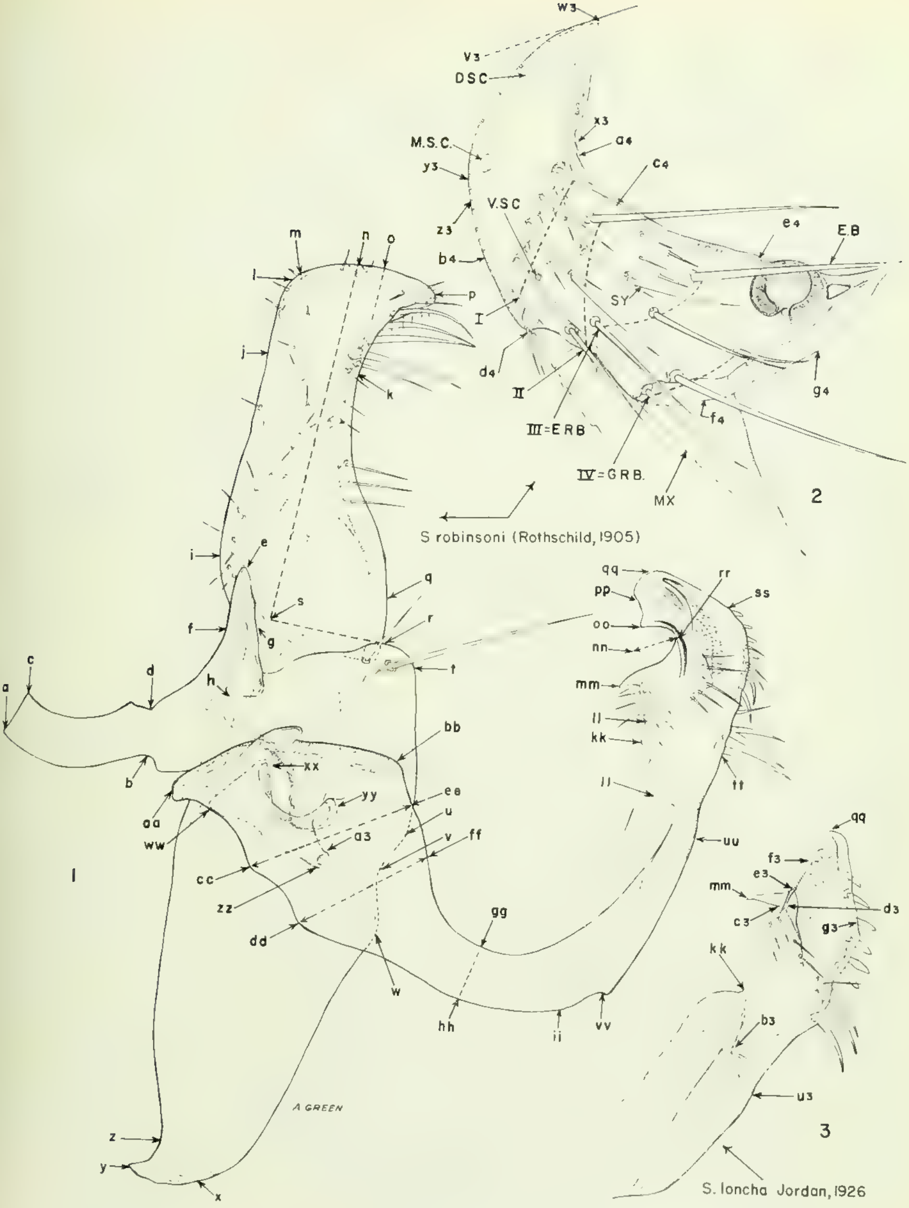
LIST OF ILLUSTRATIONS

Fig.			
1.	Clasper and sternum 9	*Medwayella*	*r. robinsoni* (Roths., 1905)
2.	Preantennal region (♂)	,,	,, ,,
3.	Distal arm of sternum 9	,,	*loncha* (Jordan, 1926)
4.	Head and prothorax (♂)	,,	*dryadosa* sp. nov.
5.	Lateral metanotal area (♂)	,,	,,
6.	Head (♀)	,,	,,
7.	Apical segments of protarsus	,,	,,
8.	Segment 5 of ♂ metatarsus	,,	,,
9.	Meso- and metathorax	,,	,,
10.	Aedeagus	,,	,,
11.	Modified abdominal segments (♂)	,,	,,
12.	Lumacaudate process	,,	,,
13.	Dorsal and ventral anal lobes (♂)	,,	,,
14.	Processes of clasper	,,	,,
15.	Spermatheca	,,	,,
16.	Anal lobes and stylet (♀)	,,	,,
17.	Processes of clasper	,,	*r. robinsoni*
18.	Clasper and sternum 9	,,	*dryadosa* sp. nov.
19.	Metatibia (♂)	,,	,,
20.	Distal arm of sternum 9	,,	,,
21.	Distal arm of sternum 9	,,	*r. robinsoni*
22.	Apical region of aedeagus (lateral aspect)	,,	*dryadosa* sp. nov.
23.	Apical region of aedeagus	,,	*r. robinsoni*
24.	Apex of aedeagus (dorsal aspect)	,,	*dryadosa* sp. nov.

25.	Apex of aedeagus (ventral aspect)	,,	,,
26.	Modified abdominal segments (♀)	,,	,,
27.	Spermatheca, genitalia and anal segments	,,	,,
28.	Sternum 8 (♂)	,,	*r. robinsoni*
29.	Sternum 8 (♂)	,,	*dryadosa* sp. nov.
30.	Segment 7 (♀)	,,	,,
31.	Genitalia (♀)	,,	,,
32.	Genitalia (♀)	,,	*r. robinsoni*
33.	Distal arm of sternum 9	,,	*arcuata* sp. nov.
34.	Processes of clasper	,,	,,
35.	Processes of clasper	,,	*angustata* sp. nov.
36.	Distal arm of sternum 9	,,	,,
37.	Modified abdominal segments (♀)	,,	,,
38.	Spermatheca, genitalia and anal segments	,,	,,
39.	Lumacaudate process	,,	,,
40.	Genitalia (♀)	,,	*javana* (Jordan, 1933)
41.	Genitalia (♀)	,,	*angustata* sp. nov.
42.	Apex of aedeagus	,,	*dryadosa* sp. nov.
43.	Sclerotized inner tube	,,	,,
44.	Apex of aedeagus	,,	*r. robinsoni*
45.	Apex of aedeagus	,,	*angustata* sp. nov.
46.	Apical region of aedeagus	,,	*r. robinsoni*
47.	Clasper and sternum 9	,,	,,
48.	Transverse suture, D.A.9	,,	,,
49.	Sternum 7 (♀)	,,	,,
50.	Lateral metanotal area (♂)	,,	,,
51.	Anal segments (♀)	,,	,,
52.	Spermatheca	,,	,,
53.	Distal arm of sternum 9	,,	*r. tiomanica* subsp. nov.
54.	Distal arm of sternum 9	,,	*r. bogora* subsp. nov.
55.	Distal arm of sternum 9	,,	*r. peregrinata* subsp. nov.
56.	Apex of aedeagus	,,	*r. tiomanica* subsp. nov.
57.	Apex of aedeagus	,,	*r. peregrinata* subsp. nov.
58.	Apex of aedeagus	,,	*r. bogora* subsp. nov.
59.	Genitalia and anal lobes (♀)	,,	*r. robinsoni*
60.	Spermatheca and sternum 7	,,	*r. peregrinata* subsp. nov.
61.	Genitalia (♀)	,,	,,
62.	Spermatheca, genitalia and sternum 7	,,	*r. bogora* subsp. nov.
63.	Proximal arm of sternum 9	,,	,,
64.	Spermatheca, genitalia and sternum 7	,,	*r. tiomanica* subsp. nov.
65.	Processes of clasper	,,	*phangi tana* subsp. nov.
66.	Processes of clasper	,,	*phangi phangi* sp. nov.
67.	Distal arm of sternum 9	,,	*p. tana* subsp. nov.
68.	Distal arm of sternum 9	,,	*p. phangi* sp. nov.
69.	Sternum 8 (♂)	,,	,,
70.	Lumacaudate process	,,	,,
71.	Apical region of aedeagus	,,	,,
72.	Tergum 8 (♀)	,,	,,
73.	Anal lobes and stylet (♀)	,,	,,
74.	Spermatheca	,,	,,
75.	Sternum 7 (♀)	,,	*p. tana* subsp. nov.
76.	Sternum 7 (♀)	,,	*p. phangi* sp. nov.
77.	Spermatheca, genitalia and anal segments	,,	,,
78.	Spermatheca (variation in aspect)	,,	*limi* sp. nov.

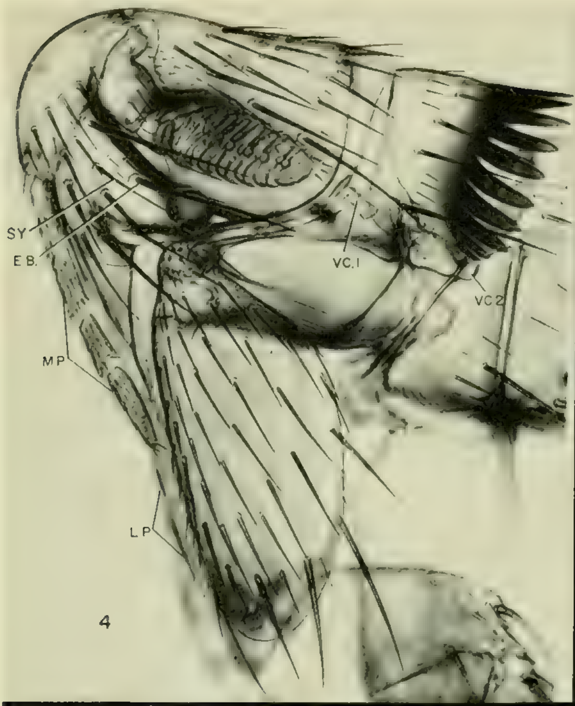
79.	Spermatheca and genitalia	,,	,,
80.	Processes of clasper	,,	,,
81.	Distal arm of sternum 9	,,	,,
82.	Apex of aedeagus	,,	,,
83.	Lumacaudate process	,,	,,
84.	Spermatheca and genitalia	,,	,,
85.	Sterna 8 and 9 (♀)	,,	,,
86.	Head and prothorax (♂)	,,	*thurmani* sp. nov.
87.	Movable finger	,,	,,
88.	Spermatheca	,,	,,
89.	Sensilium and anal segments (♀)	,,	,,
90.	Apical region of aedeagus	,,	,,
91.	Distal arm of sternum 9	,,	,,
92.	Processes of clasper	,,	,,
93.	Apical region of aedeagus	,,	*dryadosa* sp. nov.
94.	Apex of aedeagus	,,	*thurmani* sp. nov.
95.	Apex of aedeagus	,,	*javana*
96.	Sclerotized inner tube	,,	,,
97.	Apical region of aedeagus	,,	*thurmani* sp. nov.
98.	Apical region of aedeagus	,,	*arcuata* sp. nov.
99.	Sternum 7 (♀)	,,	*thurmani* sp. nov.
100.	Lateral metanotal area (♂)	,,	,,
101.	Sternum 8 (♂)	,,	,,
102.	Spermatheca and genitalia	,,	,,
103.	Spermatheca, genitalia and anal segments	,,	*calcarata* sp. nov.
104.	Head and prothorax (♂)	,,	,,
105.	Lateral metanotal area (♂)	,,	,,
106.	Lateral metanotal area (♂)	,,	*batibacula* sp. nov.
107.	Lumacaudate process	,,	*calcarata* sp. nov.
108.	Processes of clasper	,,	,,
109.	Processes of clasper	,,	*batibacula* sp. nov.
110.	Mesal aspect of F.	,,	,,
111.	Distal arm of sternum 9	,,	*calcarata* sp. nov.
112.	Distal arm of sternum 9	,,	*batibacula* sp. nov.
113.	Apex of aedeagus	,,	*calcarata* sp. nov.
114.	Apex of aedeagus	,,	*veruta* sp. nov.
115.	Apex of aedeagus	,,	*batibacula* sp. nov.
116.	Lumacaudate process	,,	,,
117.	Spermatheca and genitalia	,,	*veruta* sp. nov.
118.	Spermatheca and genitalia	,,	*loncha*
119.	Processes of clasper	,,	*veruta* sp. nov.
120.	Distal arm of sternum 9	,,	,,
121.	Sternum 8 (♂)	,,	,,
122.	Anal lobes and stylet (♀)	,,	,,
123.	Spermatheca	,,	,,
124.	Sternum 7 (♀)	,,	,,
125.	Genitalia (♀)	,,	,,
126.	Processes of clasper	,,	*loncha*
127.	Distal arm of sternum 9	,,	,,
128.	Apex of aedeagus	,,	,,
129.	Sensilium and anal segments (♀)	,,	,,
130.	Sternum 7 (♀)	,,	,,
131.	Sternum 8 (♂)	,,	,,
132.	Spermatheca	,,	,,

133.	Processes of clasper	,, *javana*
134.	Distal arm of sternum 9	,, ,,
135.	Lumacaudate process	,, ,,
136.	Sternum 7 (♀)	,, ,,
137.	Spermatheca, genitalia and anal segments	,, ,,
138.	Modified abdominal segments (♂)	,, *rhaeba* (Jordan, 1926)
139.	Modified abdominal segments (♀)	,, ,,
140.	Head and prothorax (♂)	*Lentistivalius vomerus* sp. nov.
141.	Head (♀)	,, ,,
142.	Meso- and metathorax (♂)	,, ,,
143.	Clasper and segment 9	,, ,,
144.	Distal arm of sternum 9	,, ,,
145.	Distal arm of sternum 9	,, *insolli* (Traub, 1950)
146.	Clasper and segment 9	,, ,,
147.	Modified abdominal segments (♂)	,, *vomerus* sp. nov.
148.	Aedeagus	,, ,,
149.	Metatibia (♂)	,, ,,
150.	Segment 5 of metatarsus (♂)	,, ,,
151.	Metatibia (♀)	,, ,,
152.	Apical region of aedeagus (lateral)	,, ,,
153.	Apical region of aedeagus (ventral)	,, ,,
154.	Apical region of aedeagus (lateral)	,, *insolli*
155.	Apical region of aedeagus (lateral)	,, *aestivalis* (Jameson & Sakaguti, 1954)
156.	Modified abdominal segments (♀)	,, *vomerus* sp. nov.
157.	Anal segments and stylet (♀)	,, ,,
158.	Spermatheca	,, ,,
159.	Abdominal segments 2 (♀)	,, ,,
160.	Spermatheca and genitalia	,, ,,
161.	Spermatheca (variation)	,, ,,
162.	Bursa copulatrix	*Stivalius phoberus* J. & R., 1922
163.	Spermatheca and genitalia	,, *cognatus bamus* subsp. nov.
164.	Head and prothorax (♂)	,, ,, ,,
165.	Processes of clasper	,, ,, ,,
166.	Antepygidial region (♀)	,, ,, ,,
167.	Distal arm of sternum 9	,, ,, ,,
168.	Distal arm of sternum 9	,, *c. cognatus* J. & R., 1922
169.	Distal arm of sternum 9	,, *c. spiramus* Jordan, 1926
170.	Apical region of aedeagus (lateral)	,, *c. bamus* subsp. nov.
171.	Apical region of aedeagus (ventral)	,, ,,
172.	Apical region of aedeagus	*Lentistivalius vomerus* sp. nov.
173.	Apical region of aedeagus	*Stivalius c. spiramus*
174.	Apical region of aedeagus	,, *c. bamus* subsp. nov.
175.	Sternum 7 (♀)	,, *c. spiramus*
176.	Spermatheca, genitalia and anal segments	,, *c. bamus* subsp. nov.
177.	Spermatheca and bursa copulatrix	,, ,,
178.	Bursa copulatrix	,, *c. spiramus*
179.	Spermatheca and bursa copulatrix	,, *c. cognatus*

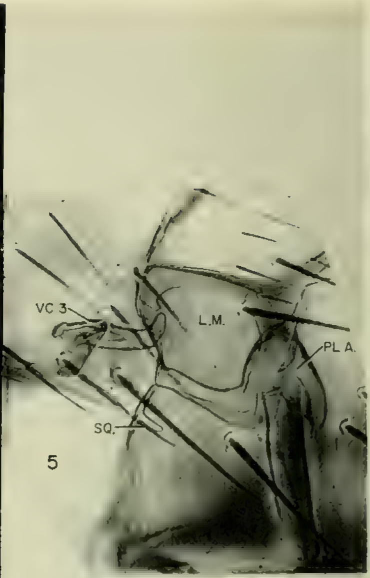

1
2
3
w3
v3
DSC
M.S.C.
y3
z3
x3
a4
c4
V.SC
e4
E.B
b4
SY
I
II
d4
III=ERB
IV=GRB.
f4
g4
MX
m
n
o
l
p
j
k
i
e
f
g
s
q
r
t
a
c
d
h
b
bb
xx
yy
aa
ww
ee
u
a3
v
ff
cc
zz
dd
w
gg
hh
ii
vv
z
y
x
qq
rr
pp
ss
oo
nn
mm
ll
kk
jj
tt
uu
f3
e3
c3
d3
g3
b3
u3
A GREEN

S robinsoni (Rothschild, 1905)

S. loncha Jordan, 1926

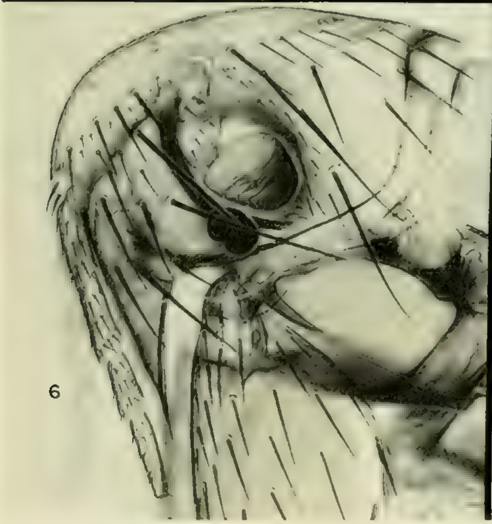

SY
E.B.
VC.1
VC 2
MP
LP

4

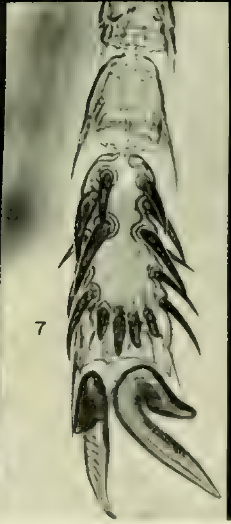

VC 3
L.M.
PL A.
SQ.

5

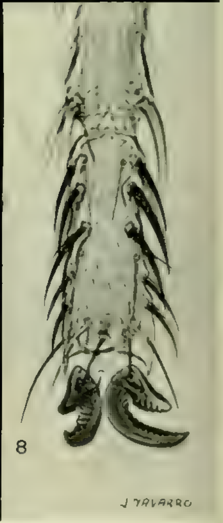
FIGS 4–8
M. DRYADOSA N SP.



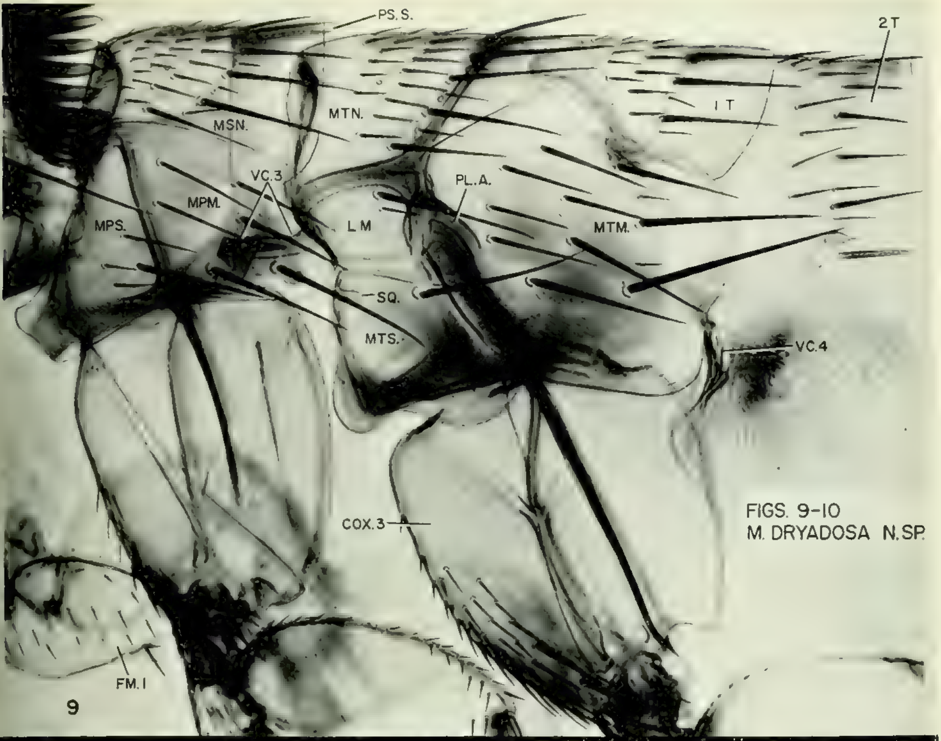
6



7

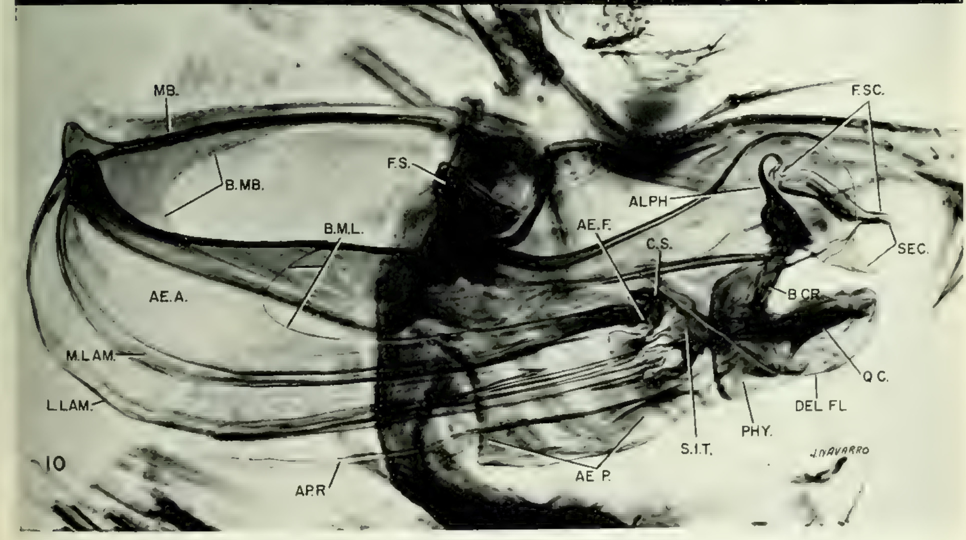


8

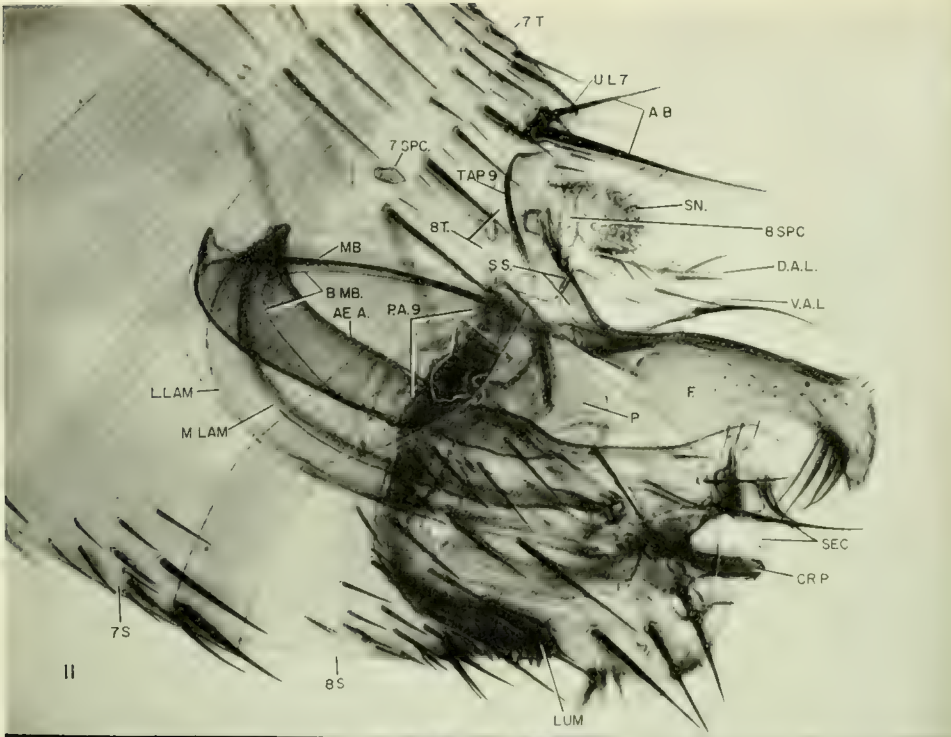

PS. S.
2T
MTN.
I T
MSN.
VC.3
PL. A.
MPM.
L M
MTM.
MPS.
SQ.
MTS.
VC.4
COX.3
FM. I

9

FIGS. 9–10
M. DRYADOSA N. SP.

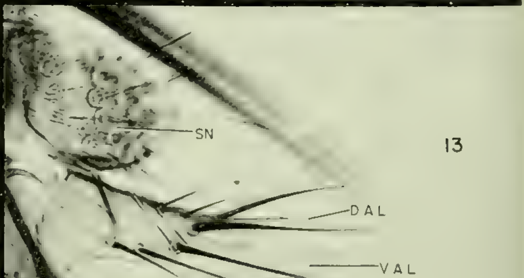

MB.
F.SC.
B.MB.
F.S.
ALPH
B.M.L.
AE.F.
C.S.
SEC.
AE.A.
B CR.
M.LAM.
Q C.
L.LAM.
DEL FL
PHY.
S.I.T.
AE P.
APR
J. NAVARRO

10

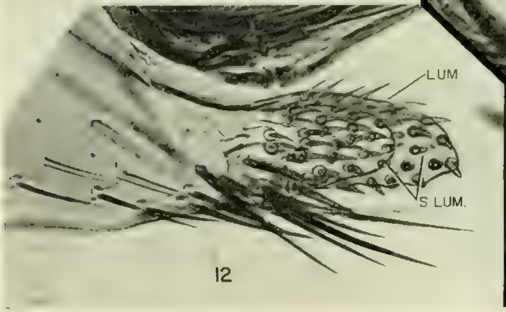

7 T
U L 7
A B
7 SPC.
TAP 9
SN.
8 SPC
8T.
MB
S S.
D.A.L.
V.A.L
B MB.
AE A.
P.A.9
L LAM
M LAM
F
P
SEC
CR P
7S
8S
LUM

11

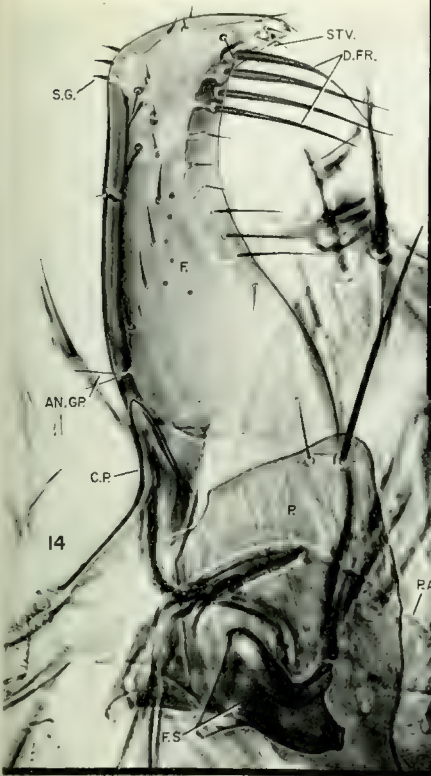
FIGS. 11-13
M. DRYADOSA N. SP.



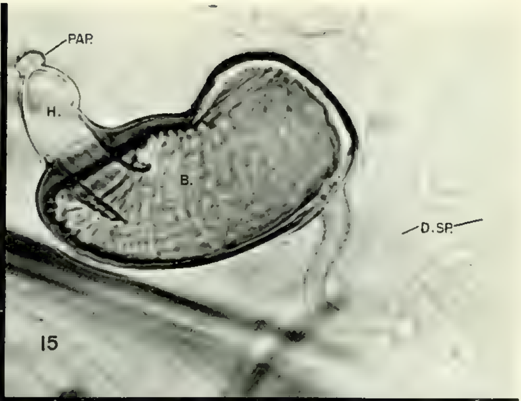
13



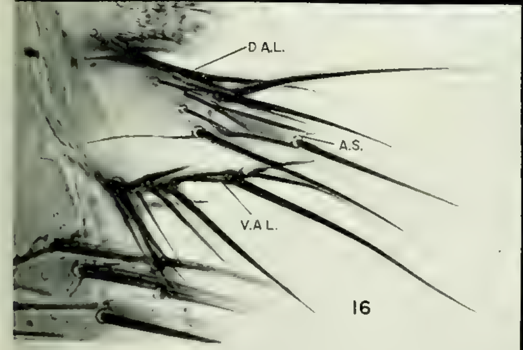
12


STV.
D.FR.
S.G.
F.
AN.GP.
C.P.
P.
P.A.9
F.S.

14

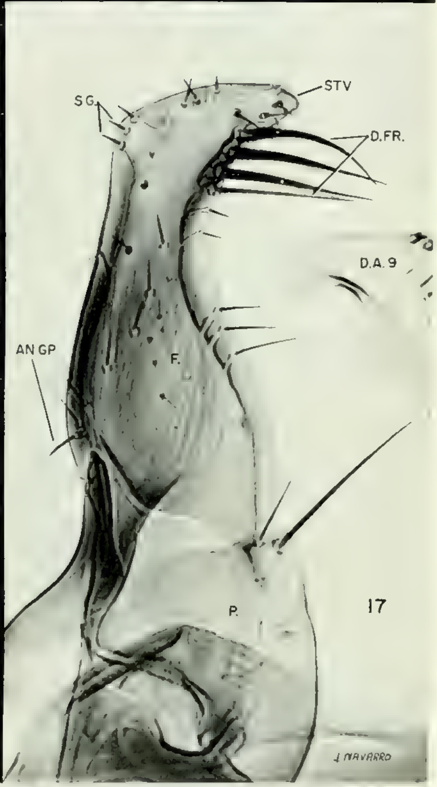


15



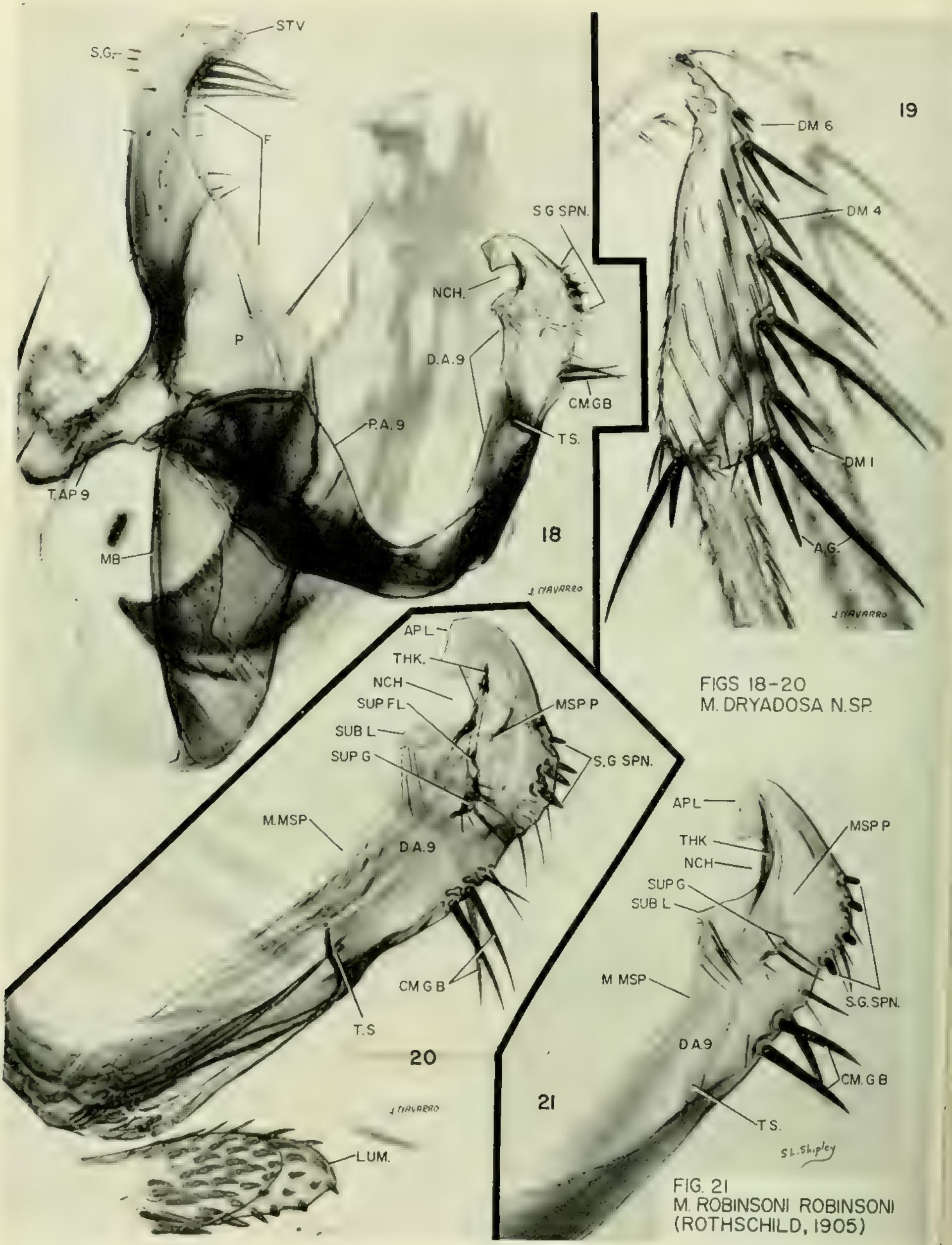
16

FIGS. 14–16
M. DRYADOSA N.SP.


S.G.
STV
D.FR.
D.A.9
AN.GP.
F.
P.
J. NAVARRO

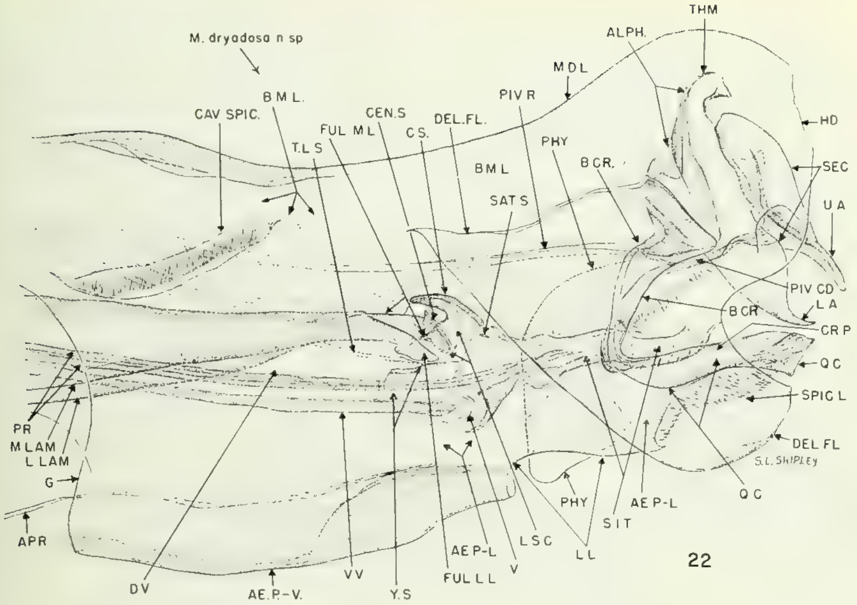
17

FIG. 17
M. ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)

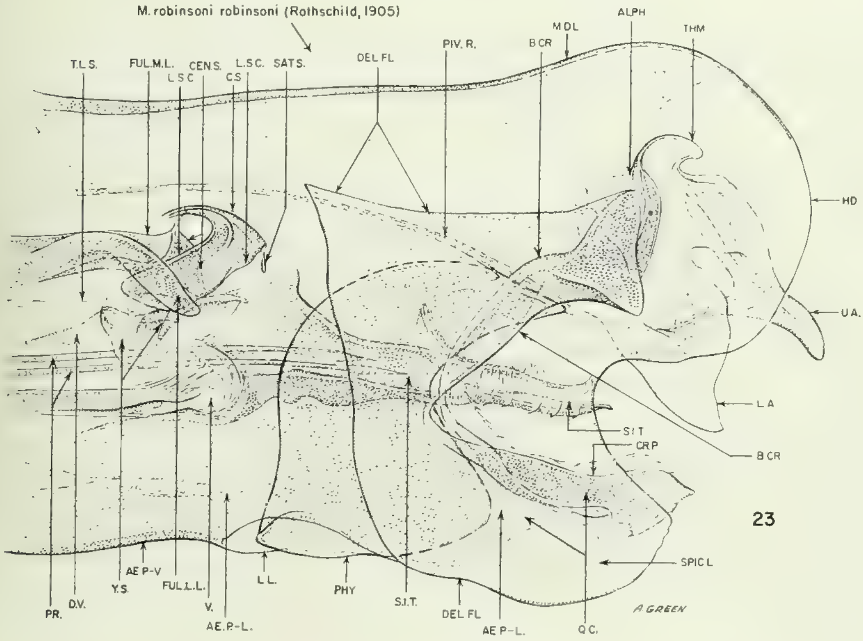

STV
S.G.
F
P
S G SPN.
NCH.
D.A.9
CM.G B
T.S.
P.A.9
T.AP 9
MB
18
J. NAVARRO
DM 6
19
DM 4
DM 1
A.G.
J. NAVARRO
AP L
THK.
NCH
SUP FL
MSP P
SUB L
SUP G
S.G SPN.
M.MSP
D A.9
CM G B
T.S
20
J. NAVARRO
LUM.
AP L
MSP P
THK
NCH
SUP G
SUB L
M MSP
S.G. SPN.
D A.9
CM. G B
T S.
21
S.L. Shipley

FIGS 18–20
M. DRYADOSA N.SP.

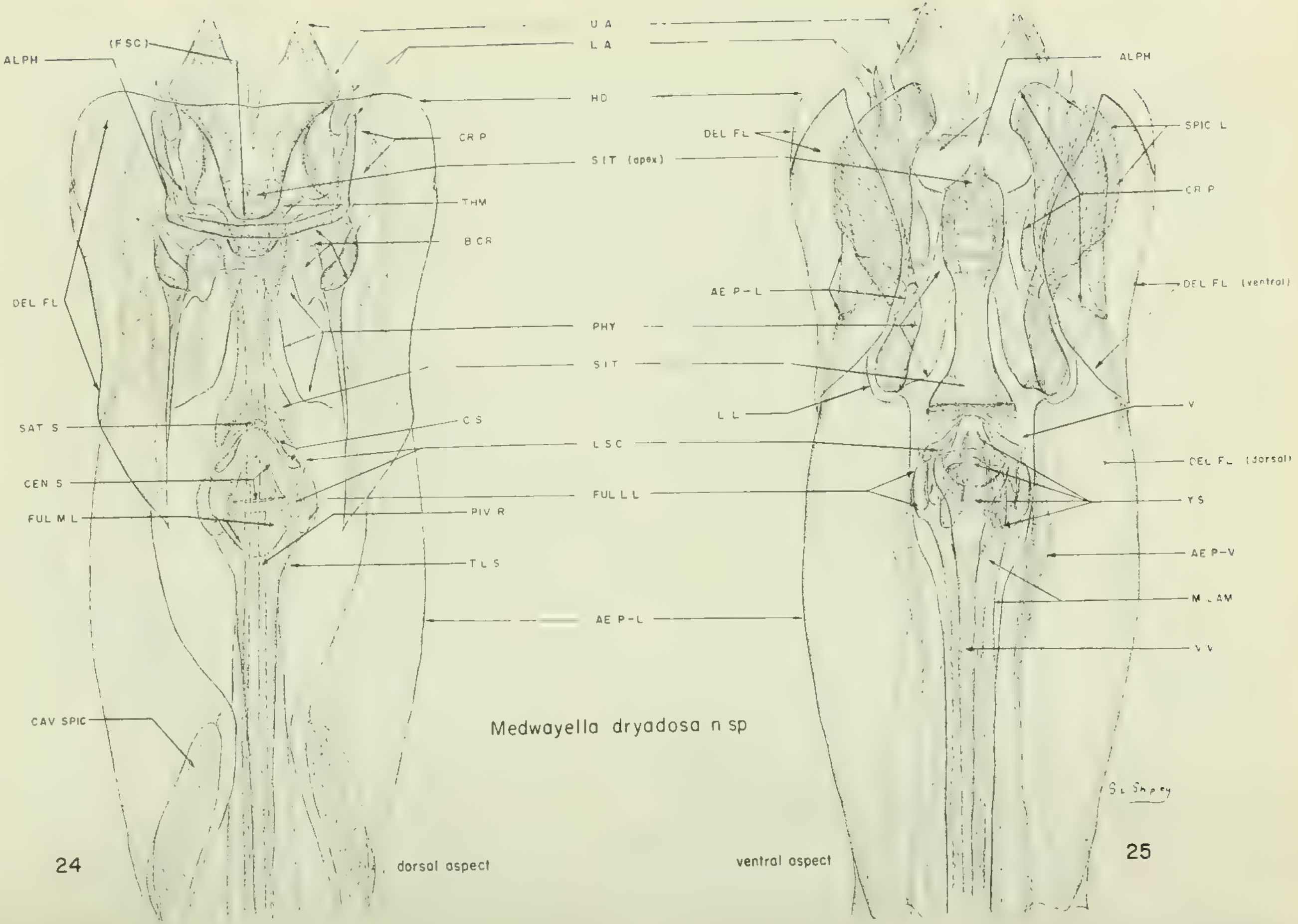
FIG. 21
M. ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)


M. dryadosa n sp
THM
ALPH.
M D L
B M L.
CAV SPIC.
CEN.S
FUL M L
C S.
DEL.FL.
PIV R
T.L S
B M L
PHY
B CR.
HD
SEC
SATS
U A
PIV CD
B CR
L A
CR P
Q C
SPIC L
PR
M LAM
L LAM
G
APR
DEL FL
S.L. SHIPLEY
PHY
AE P-L
Q C
S I T
L S C
L L
AE P-L
V
DV
VV
FUL L L
AE.P.-V.
Y.S

22


M. robinsoni robinsoni (Rothschild, 1905)
M DL
ALPH
THM
PIV. R.
B CR
DEL FL
T.L.S.
FUL.M.L.
CEN.S.
L S C
L.S.C.
C S
SATS.
HD
U.A.
L A
S I T
CRP
B CR
SPIC L
PR.
D.V.
AE P-V
Y.S.
FUL.L.L.
V.
AE.P.-L.
L.L.
PHY
S.I.T.
DEL FL
AE P-L.
Q C.
A GREEN

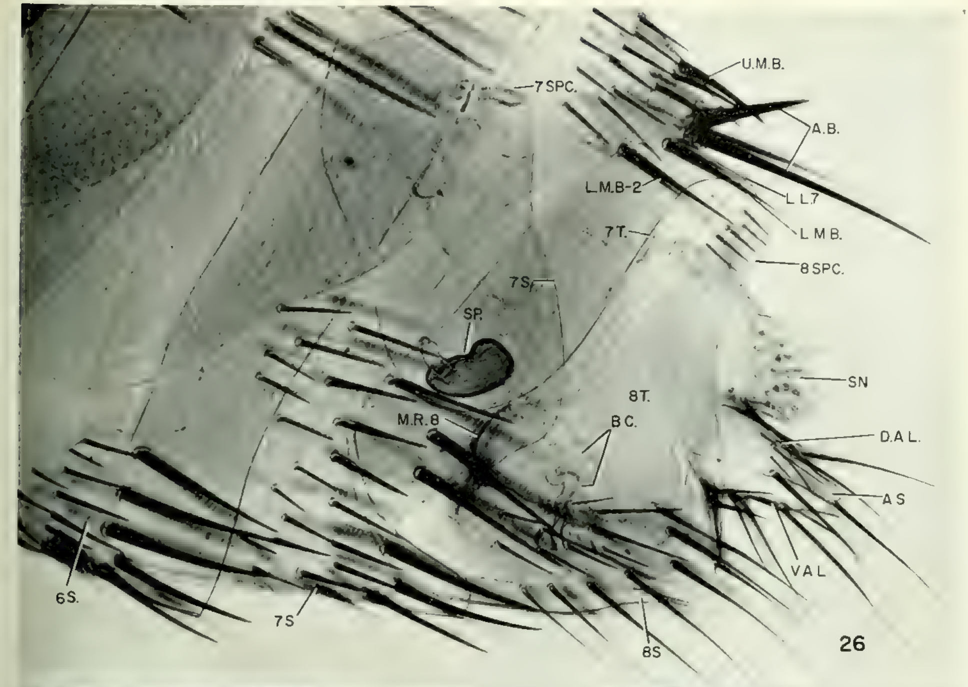
23


ALPH
(FSC)
U A
L A
HD
CR P
S IT (apex)
THM
B CR
DEL FL
PHY
S IT
SAT S
C S
L S C
CEN S
FUL L L
FUL M L
PIV R
T L S
AE P-L
CAV SPIC
ALPH
DEL FL
SPIC L
CR P
AE P-L
DEL FL (ventral)
L L
V
DEL FL (dorsal)
Y S
AE P-V
M LAM
V V
S L Shpey

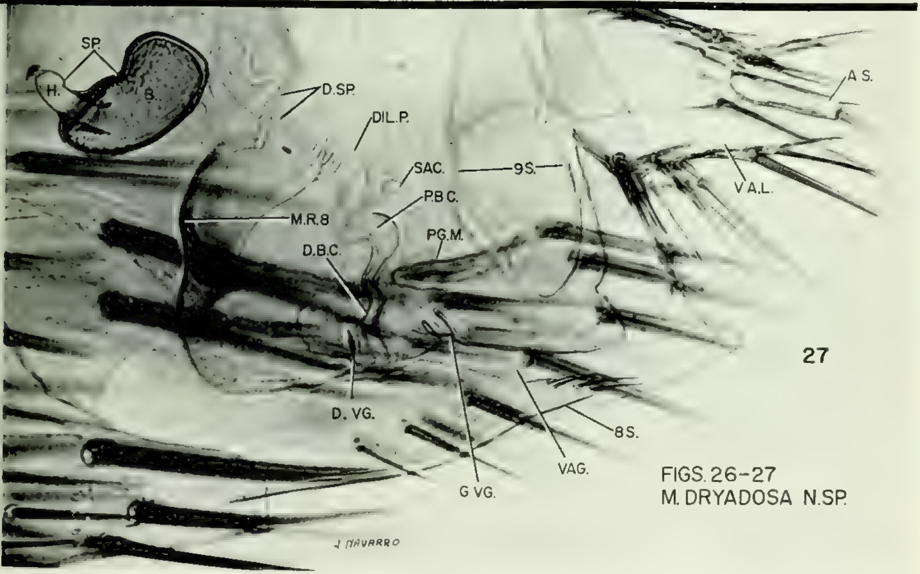
24 dorsal aspect

25 ventral aspect

Medwayella dryadosa n sp


U.M.B.
7 SPC.
A.B.
L.M.B-2
L L.7
L M B.
7T.
8 SPC.
7S
SP.
SN
8T.
M.R.8
B C.
D.A L.
A S
V A L
6S.
7S
8S

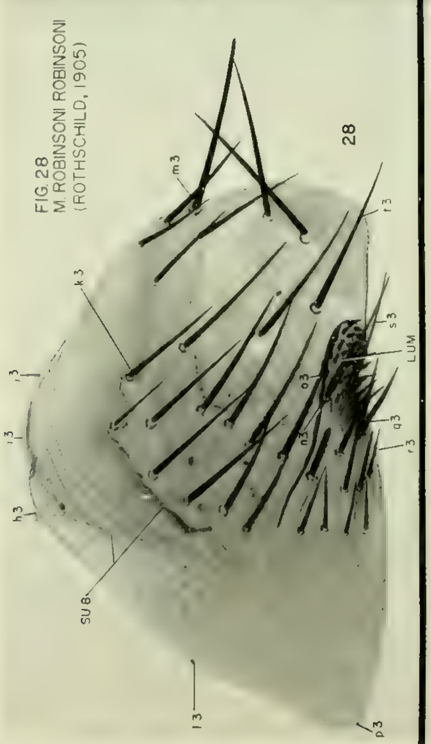
26


SP.
H.
B.
D.SP.
DIL.P.
A S.
SAC.
9S.
V A.L.
P.B C.
M.R.8
P.G.M.
D.B.C.
D. VG.
8S.
VAG.
G VG.
J NAVARRO

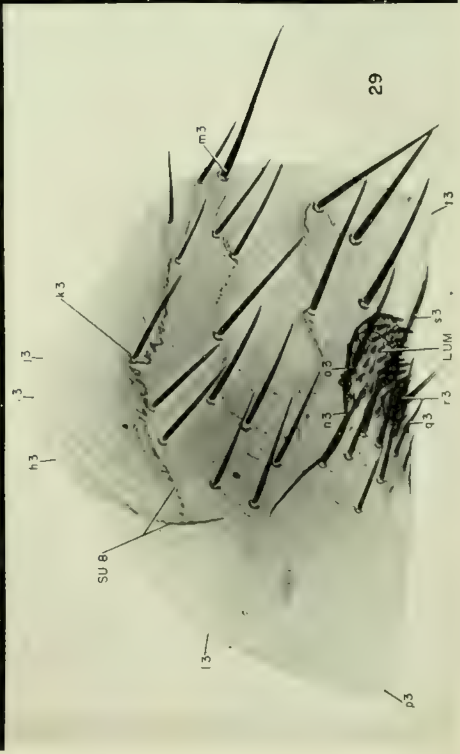
27

FIGS. 26–27
M. DRYADOSA N.SP.

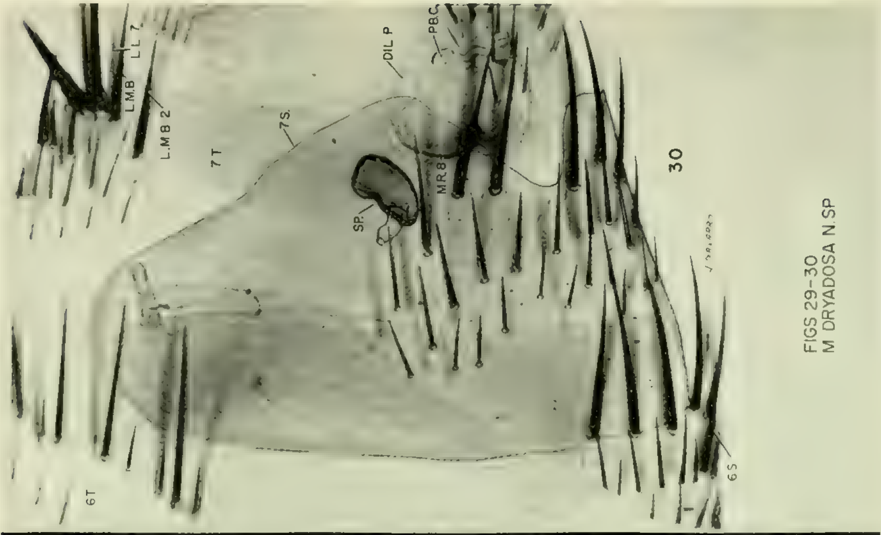
FIG. 28
M. ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)


m3
l3
k3
i3
j3
h3
SU 8
LUM
s3
o3
n3
q3
r3
l3
p3

28

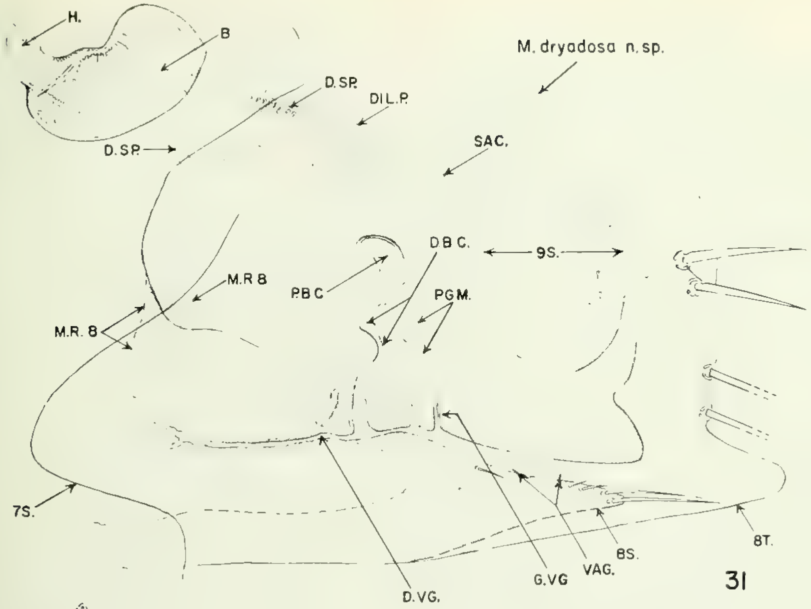

m3
l3
k3
i3
j3
h3
SU 8
s3
LUM
o3
r3
n3
q3
l3
p3

29

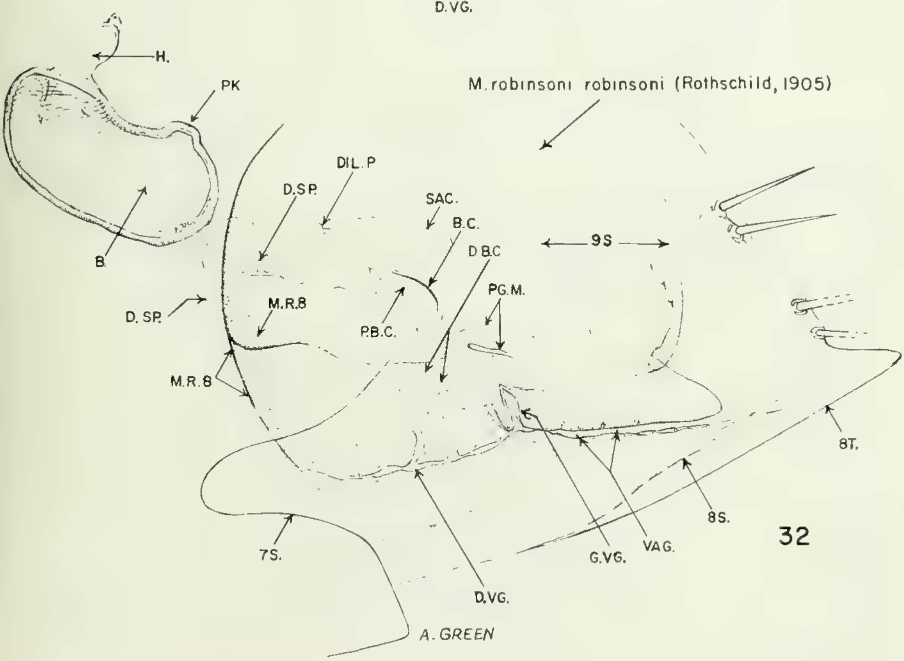

LL 7
L.M.B
L.M.B 2
DIL P
PBC
7S
7T
MR.8
SP
6T
6S

30

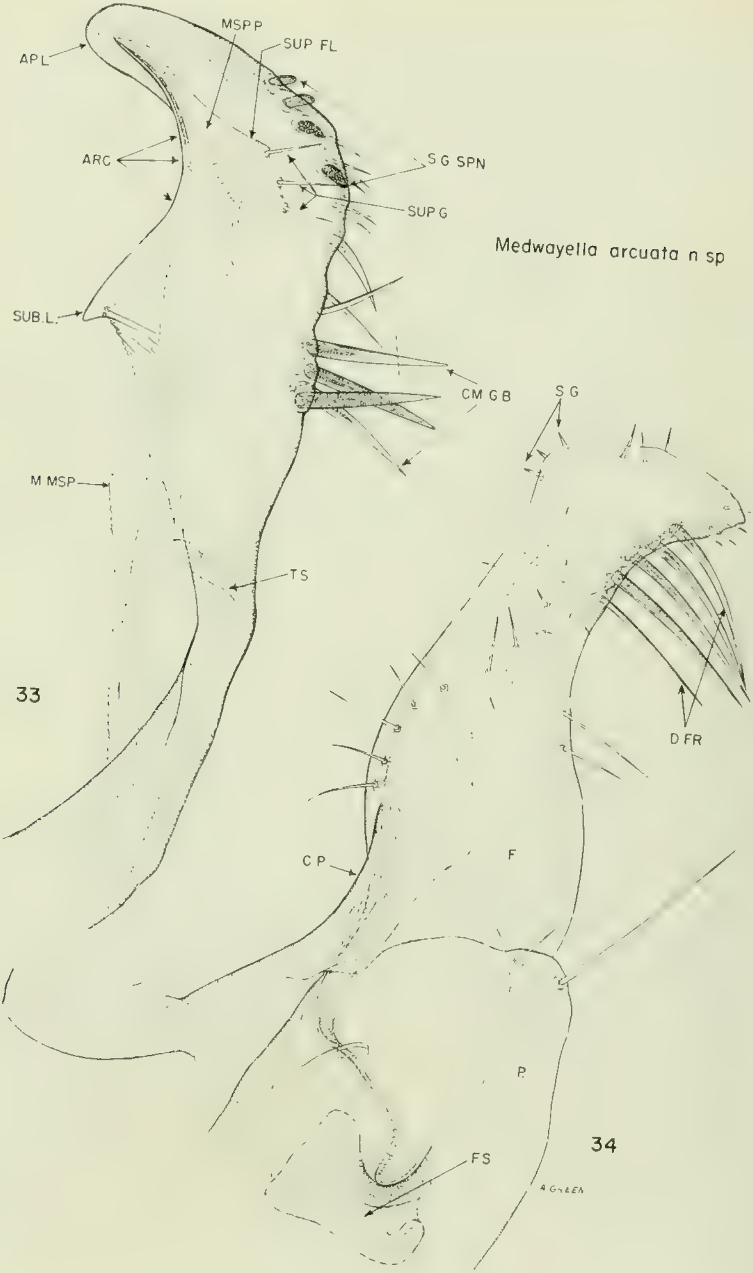
FIGS 29–30
M DRYADOSA N.SP


M. dryadosa n.sp.
H.
B
D.SP.
DIL.P.
D.SP.
SAC.
D.B.C.
9S.
P.B.C
PG.M.
M.R.8
M.R.8
7S.
D.VG.
G.VG
VAG.
8S.
8T.

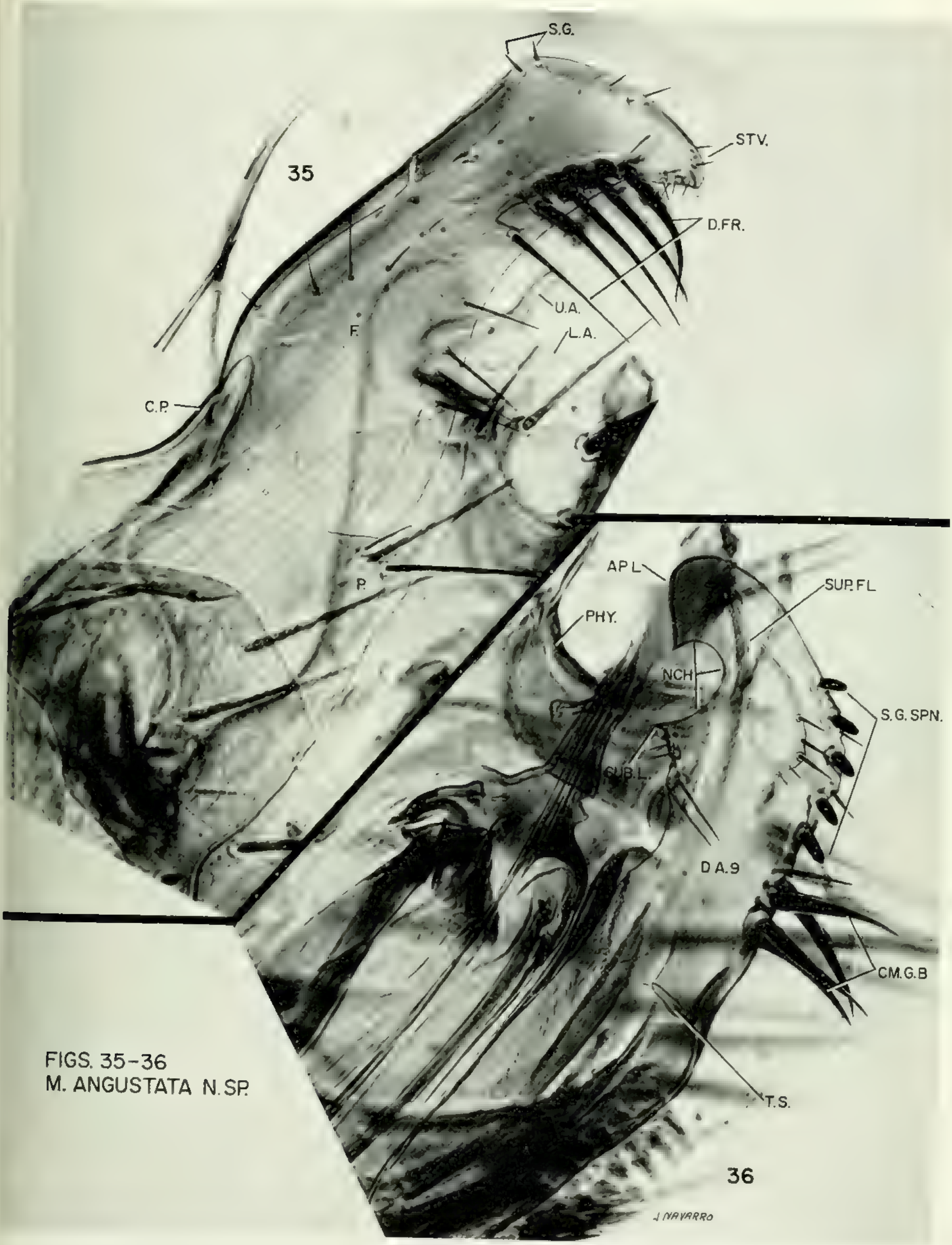
31


M. robinsoni robinsoni (Rothschild, 1905)
H.
PK
B.
DIL.P
D.SP.
SAC.
B.C.
D.B.C
9S
D. SP.
M.R.8
P.B.C.
PG.M.
M.R.8
8T.
8S.
7S.
G.VG.
VAG.
D.VG.
A. GREEN

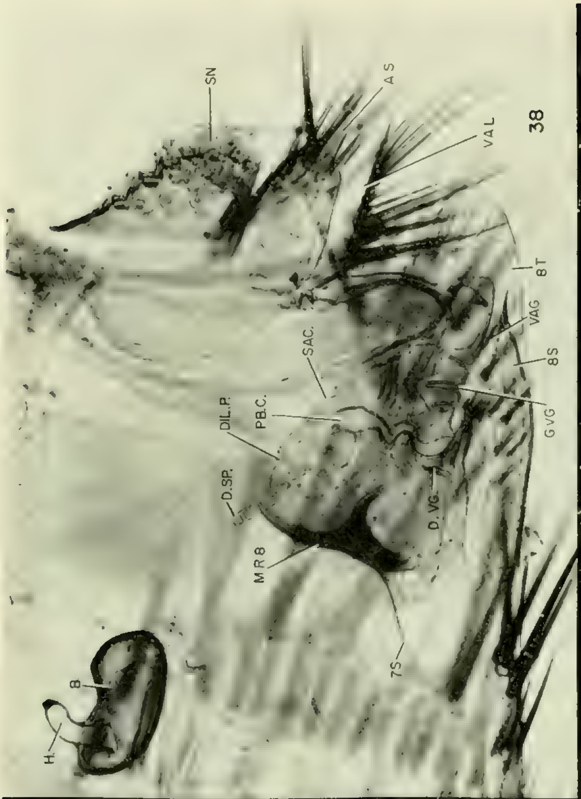
32


APL
MSPP
SUP FL
ARC
S G SPN
SUP G
SUB.L.
CM G B
S G
M MSP
TS
D FR
C P
F
P
FS
33
34

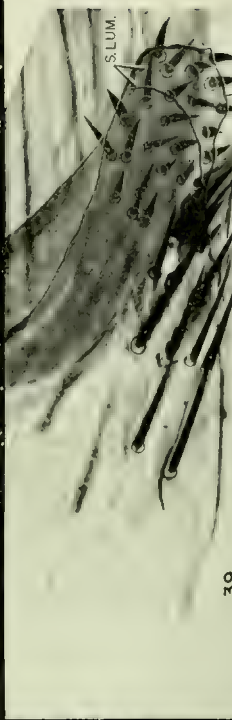
Medwayella arcuata n sp


S.G.
STV.
35
D.FR.
U.A.
L.A.
F.
C.P.
P.
AP.L.
SUP.FL.
PHY.
NCH.
S.G.SPN.
SUB.L.
D.A.9
CM.G.B
T.S.
36
J NAVARRO

FIGS. 35–36
M. ANGUSTATA N.SP.

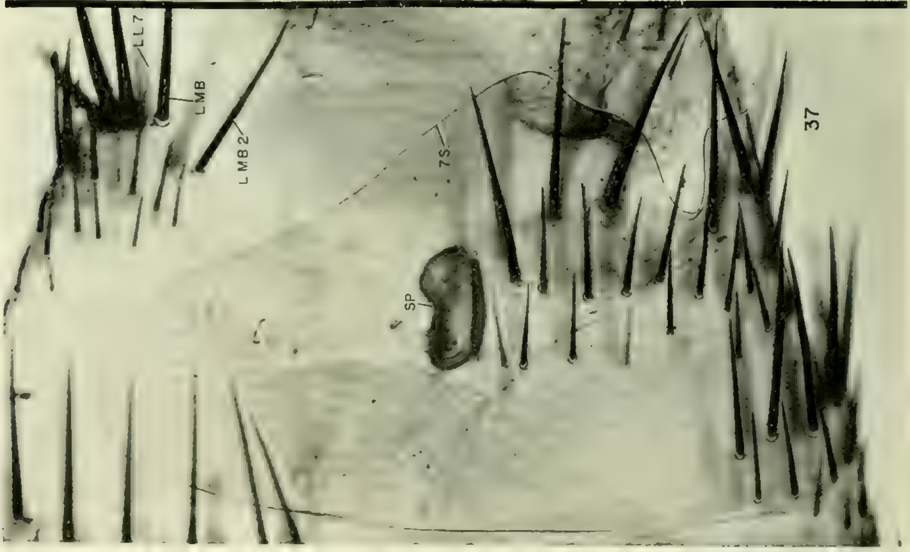

SN
AS
VAL
8T
VAG
8S
GVG
SAC.
PB.C.
DIL.P.
D.SP.
D.VG.
MRB
7S
B
H.

38



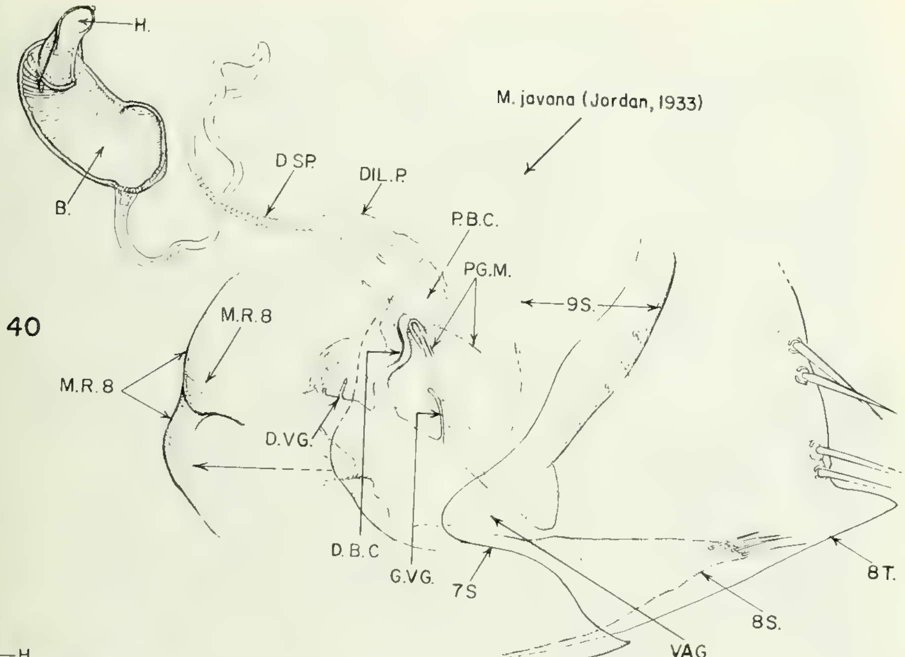
39

J NAVARRO


LL7
LMB
LMB2
7S
SP

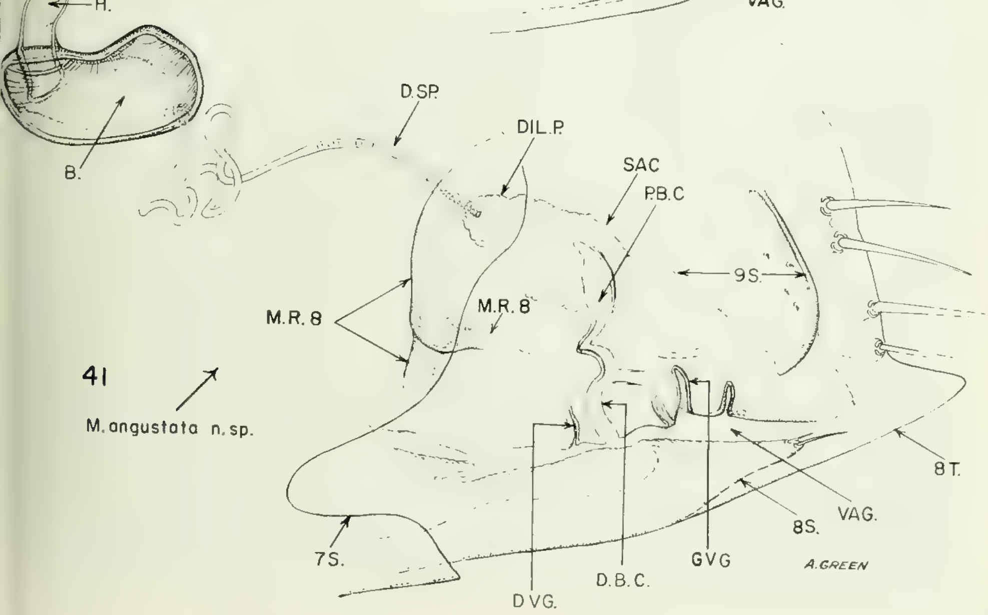
37

FIGS. 37–39
M. ANGUSTATA N.SP.


H.
B.
D.SP.
DIL.P.
P.B.C.
PG.M.
9S.
M.R.8
M.R.8
D.VG.
D.B.C
G.VG.
7S
8T.
8S.
VAG.

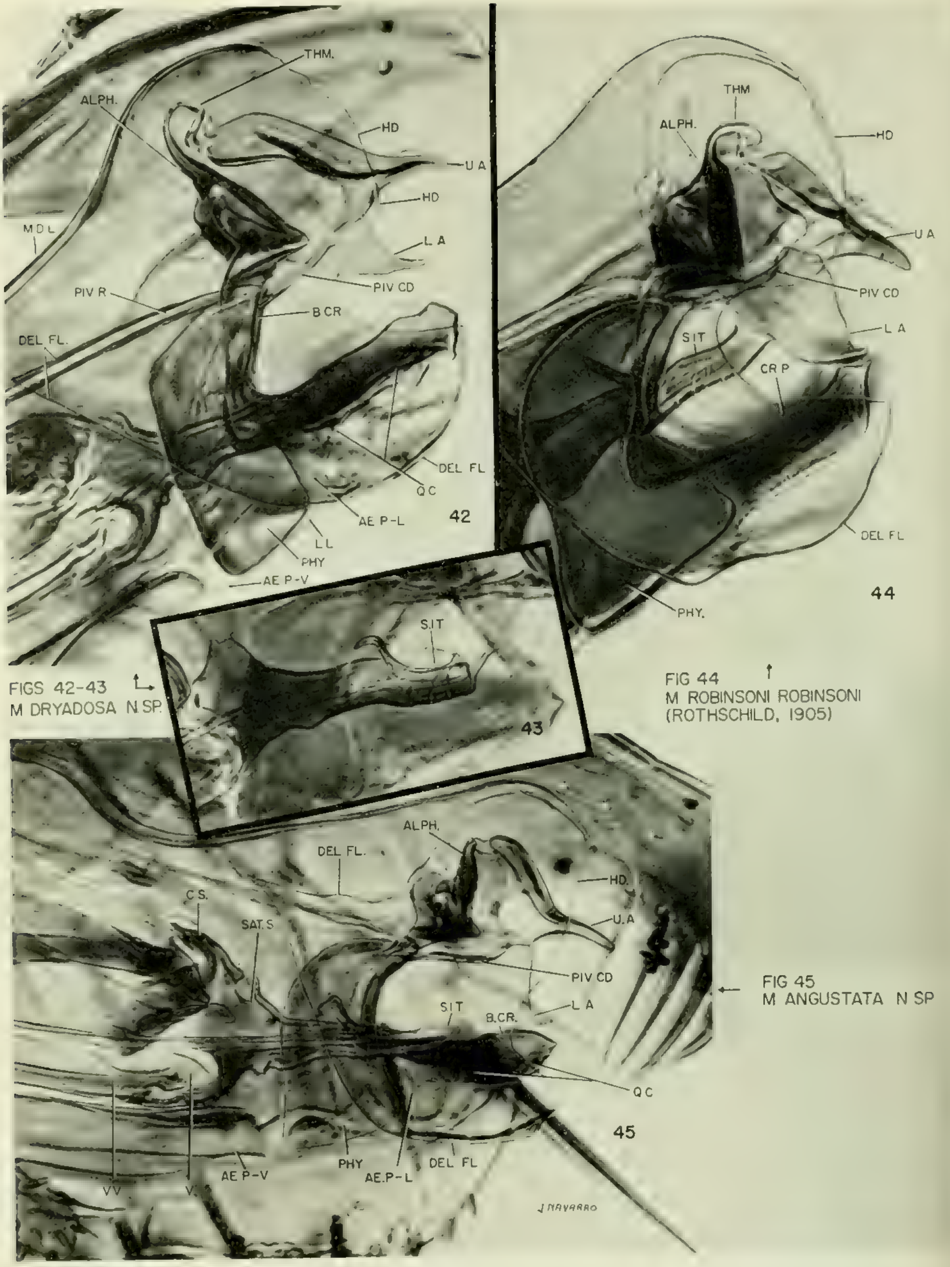
40

M. javana (Jordan, 1933)


H.
B.
D.SP.
DIL.P.
SAC
P.B.C
9S.
M.R.8
M.R.8
7S.
D.VG.
D.B.C.
GVG
VAG.
8S.
8T.
A.GREEN

41

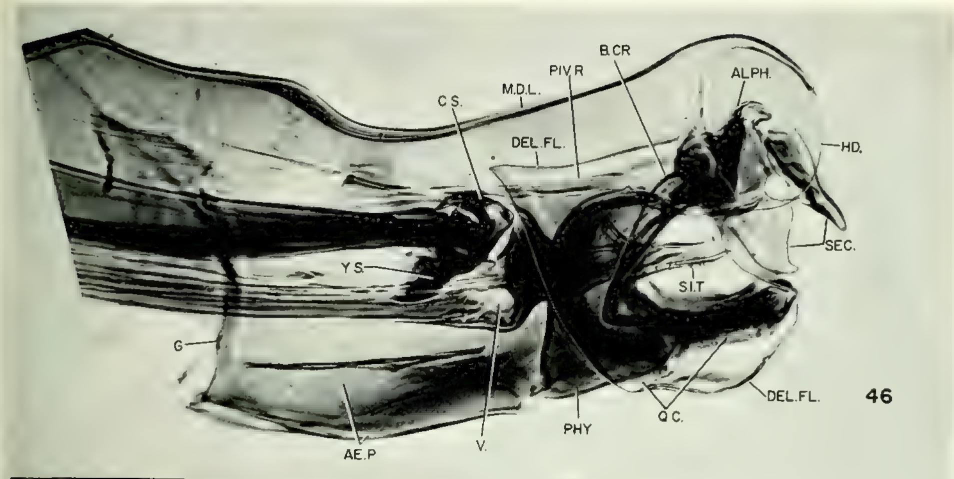
M. angustata n. sp.

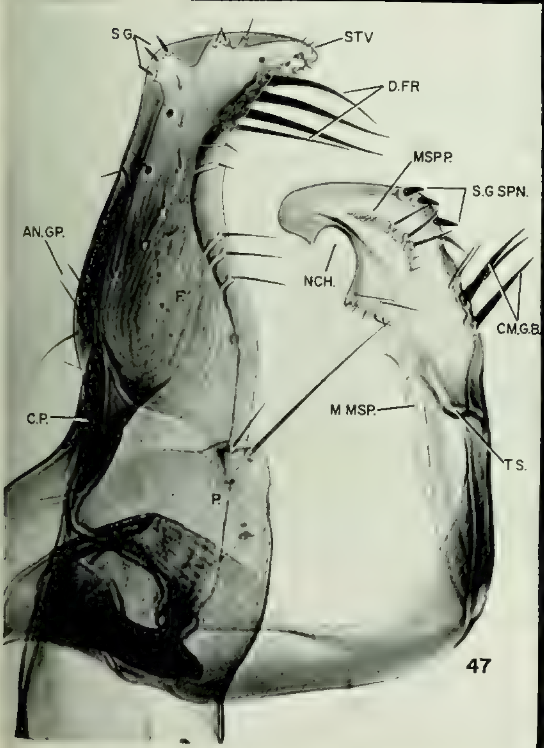

THM.
ALPH.
HD
U A
HD
M D L
L A
PIV R
PIV CD
B CR
DEL FL.
DEL FL
Q C
AE P-L
42
L L
PHY
AE P-V
S.I T
43
THM
ALPH.
HD
U A
PIV CD
L A
S.I T
CR P
DEL FL
44
PHY.
ALPH.
DEL FL.
HD.
C S.
U. A
SAT. S
PIV CD
L A
S.I T
B.CR.
Q C
45
V V
V.
AE P-V
PHY
AE.P-L
DEL FL
J NAVARRO

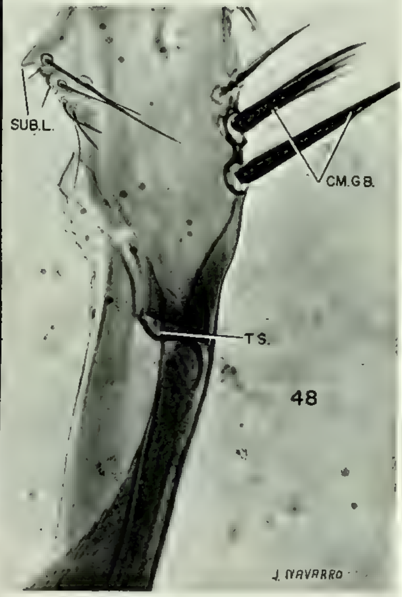
FIGS 42-43
M DRYADOSA N SP

FIG 44
M ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)

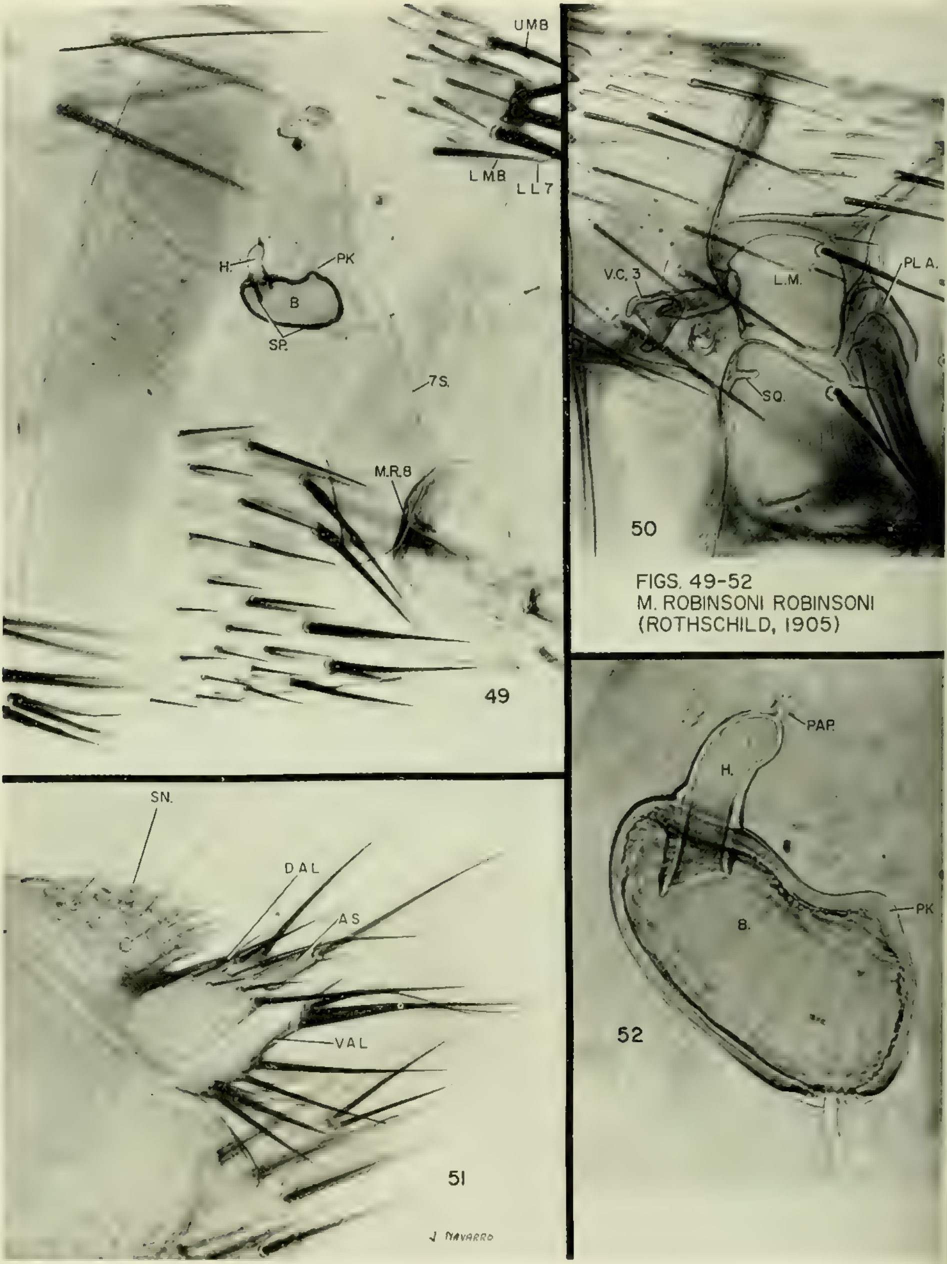
FIG 45
M ANGUSTATA N SP


B.CR
PIV.R
ALPH.
M.D.L.
C.S.
HD.
DEL.FL.
SEC.
Y.S.
SI.T
G
DEL.FL.
46
Q.C.
PHY
AE.P
V.


S.G.
STV
D.FR
MSP.P.
S.G.SPN.
AN.GP.
NCH.
F.
CM.G.B.
M.MSP.
C.P.
T.S.
P.
47


SUB.L.
CM.G.B.
T.S.
48
J. NAVARRO

FIGS. 46-48
M. ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)


UMB
LMB
LL7
H.
PK
B
SP.
7S.
M.R.8
49
V.C.3
L.M.
PL A.
SQ.
50
SN.
DAL
AS
VAL
51
PAP.
H.
PK
B.
52
J. NAVARRO

FIGS. 49-52
M. ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)

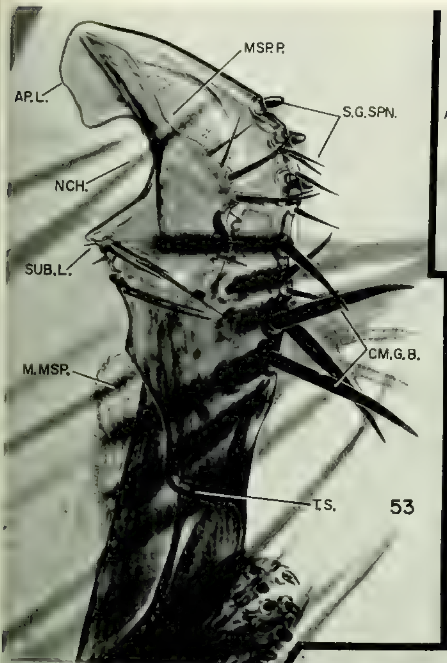

MSP.P.
AP.L.
S.G.SPN.
NCH.
SUB.L.
CM.G.B.
M.MSP.
T.S.
53

FIG. 53
M. R. TIOMANICA N.SSP.

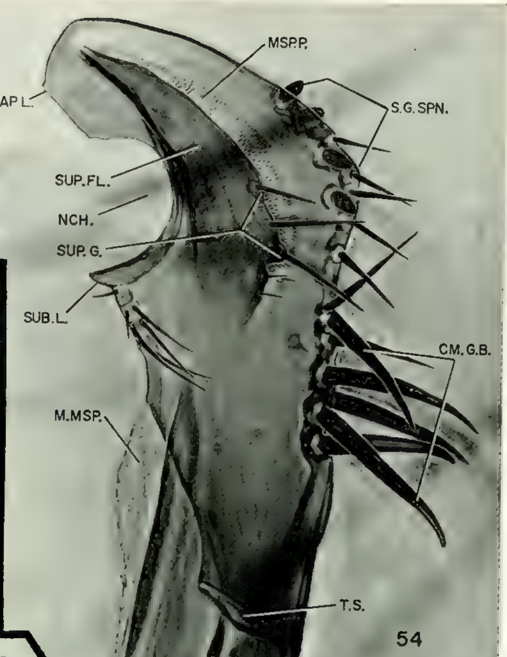

MSP.P.
AP.L.
S.G.SPN.
SUP.FL.
NCH.
SUP.G.
SUB.L.
CM.G.B.
M.MSP.
T.S.
54

FIG. 54
M. ROBINSONI BOGORA N.SSP.

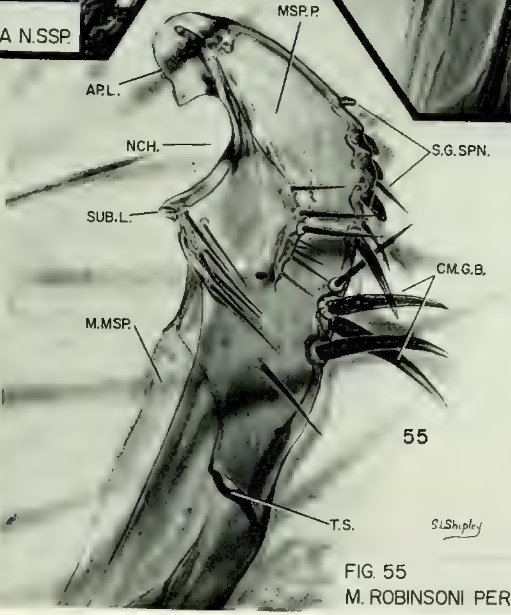

MSP.P.
AP.L.
NCH.
S.G.SPN.
SUB.L.
CM.G.B.
M.MSP.
55
T.S.
S.L.Shipley

FIG. 55
M. ROBINSONI PEREGRINATA N.SSP.

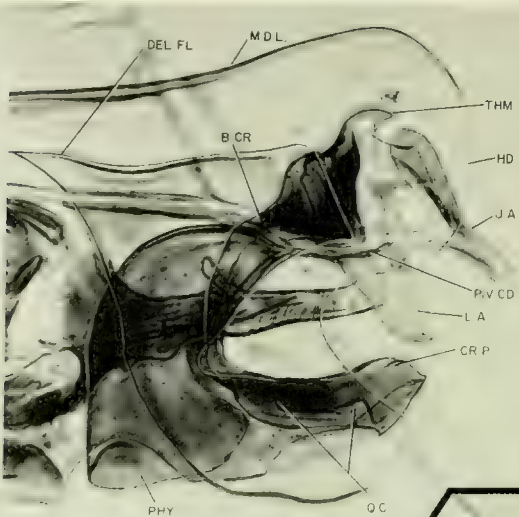
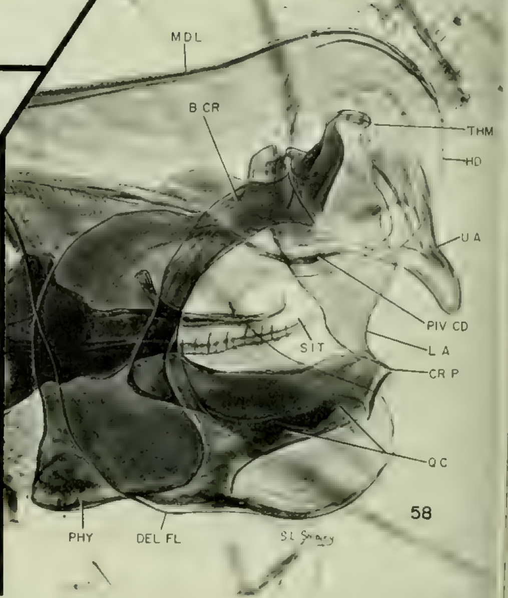

DEL FL
M D L.
THM
B CR
HD
U A
PIV CD
L A
CR P
PHY
Q C
56

FIG. 56
M. ROBINSONI TIOMANICA N SSP

FIG 58
M ROBINSONI BOGORA N SSP


M D L
B CR
THM
HD
U A
PIV CD
S I T
L A
CR P
Q C
PHY
DEL FL
58

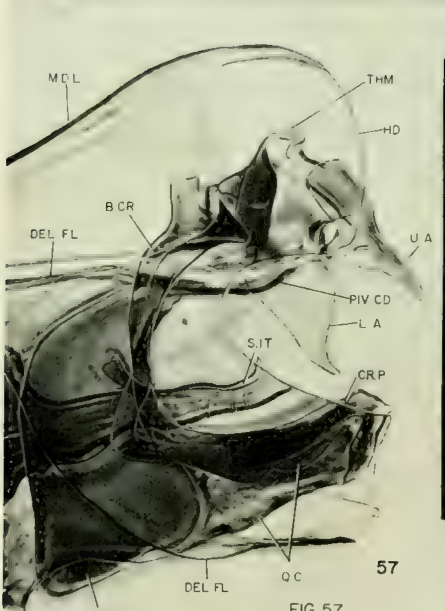

M D L
THM
HD
B CR
DEL FL
U A
PIV CD
L A
S.IT
CR P
Q C
DEL FL
PHY
57

FIG 57
M. ROBINSONI PEREGRINATA N SSP.

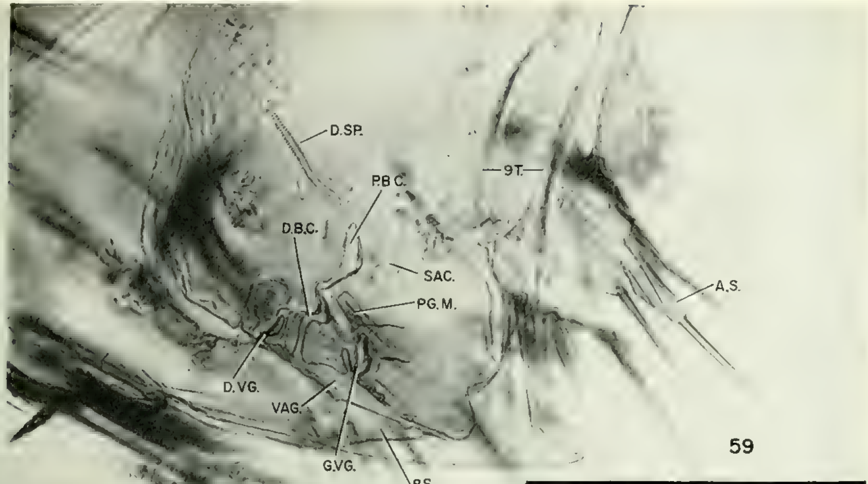
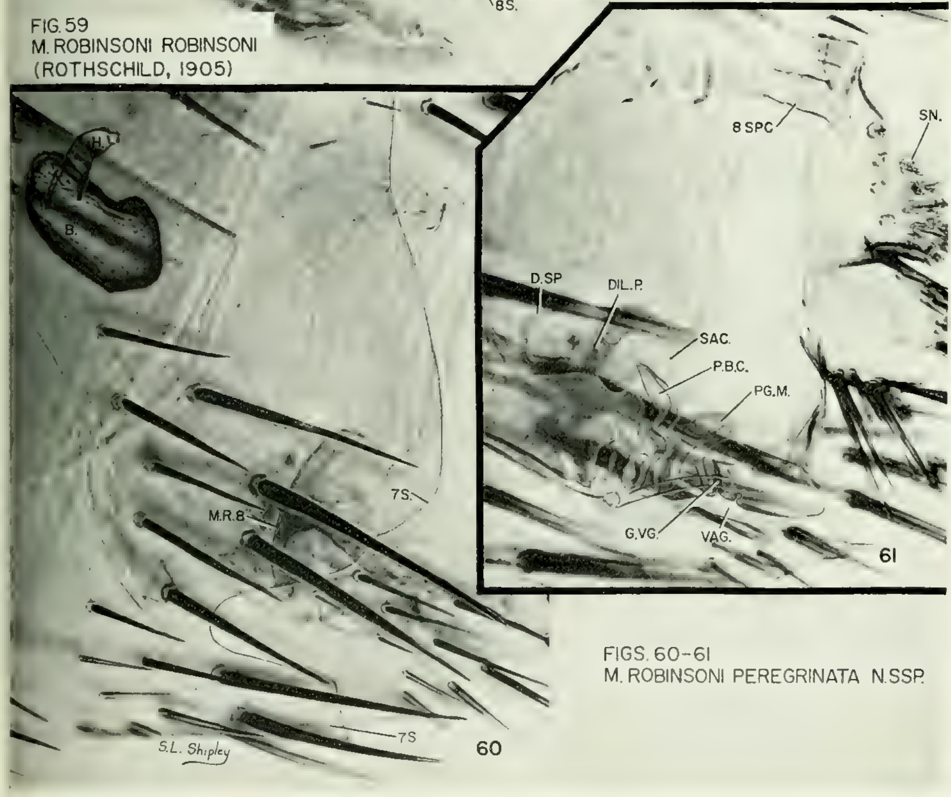
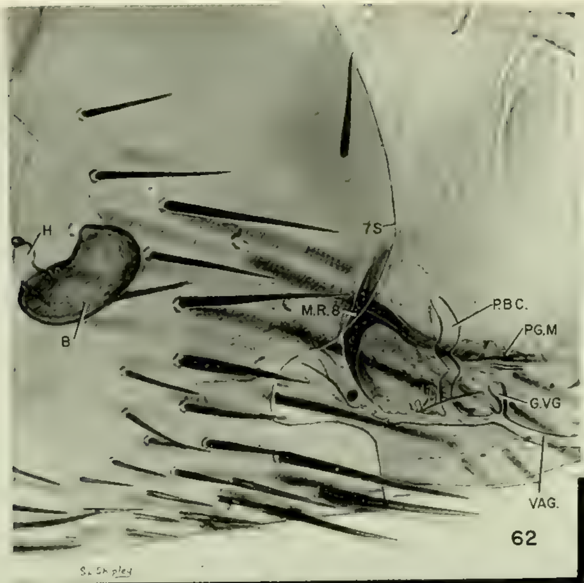

D.SP.
P.B.C.
9T.
D.B.C.
SAC.
A.S.
PG.M.
D.VG.
VAG.
G.VG.
8S.
59

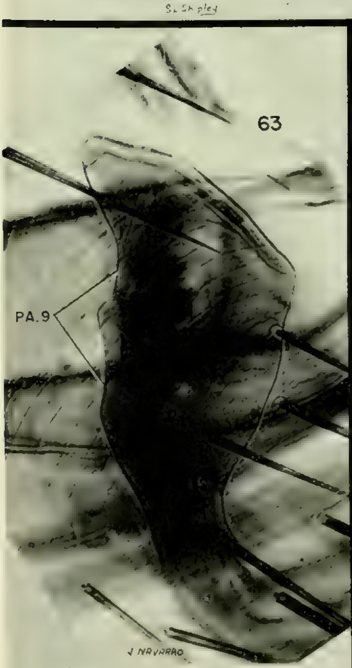
FIG. 59
M. ROBINSONI ROBINSONI
(ROTHSCHILD, 1905)


H.
B.
7S.
M.R.8
7S
S.L. Shipley
60
8 SPC
SN.
D.SP
DIL.P.
SAC.
P.B.C.
PG.M.
G.VG.
VAG.
61

FIGS. 60–61
M. ROBINSONI PEREGRINATA N.SSP.

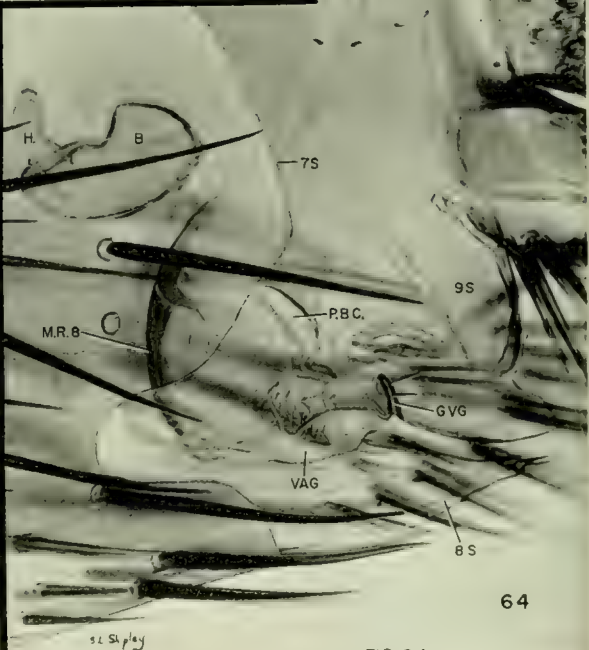

H
B
7S
M.R.8
P.B.C.
PG.M
G.VG
VAG.
S L Shipley

62


PA.9
J NAVARRO

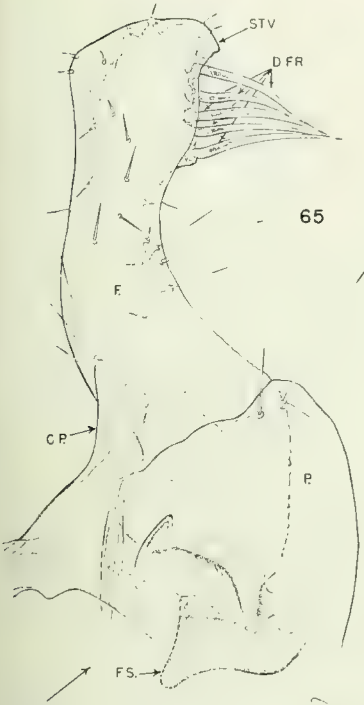
63

FIGS. 62-63
M. ROBINSONI BOGORA N SSP.

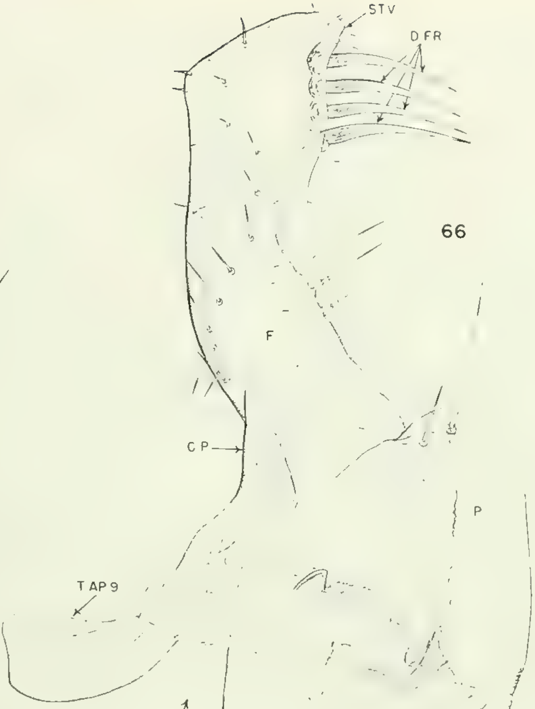

H.
B
7S
9S
P.B.C.
M.R.8
GVG
VAG
8S
S L Shipley

64

FIG. 64
M.R. TIOMANICA N.SSP.


STV
D FR
F
C P
P
F S

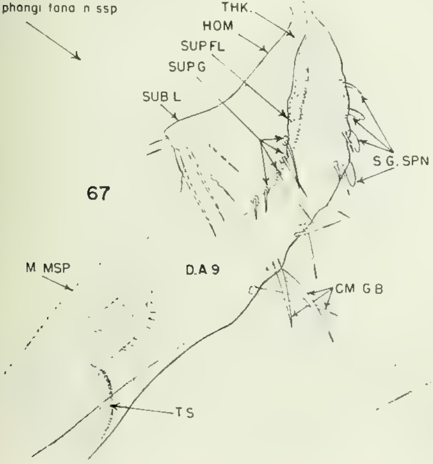
65


STV
D FR
F
C P
P
T AP 9
FS

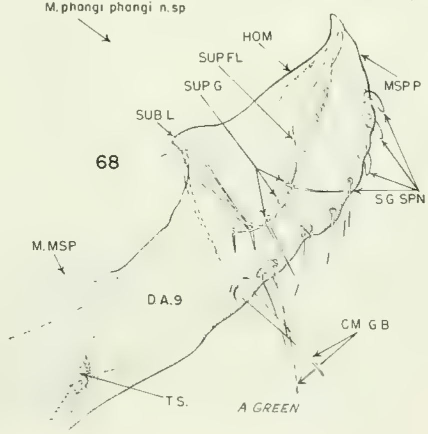
66

M phangi tana n ssp

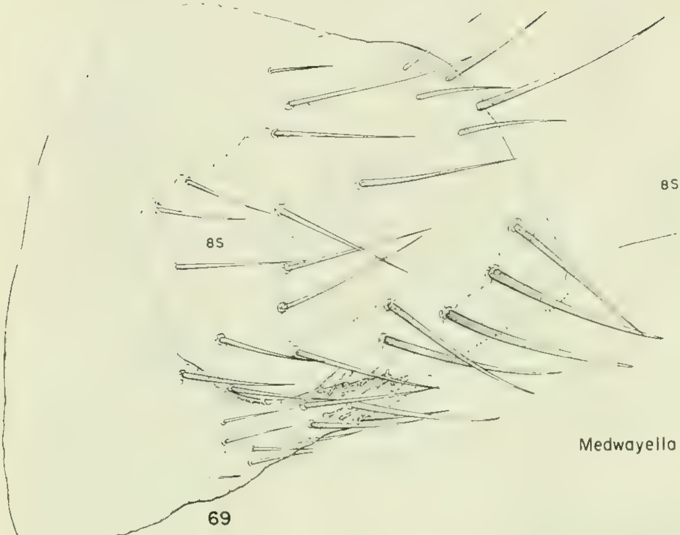
M. phangi phangi n.sp


THK.
HOM
SUP FL
SUP G
SUB L
S G. SPN
M MSP
D.A 9
CM G B
T S

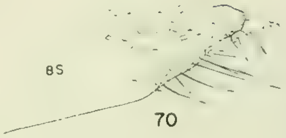
67


HOM
SUP FL
SUP G
SUB L
MSP P
S G SPN
M. MSP
D A.9
CM G B
T S.
A GREEN

68

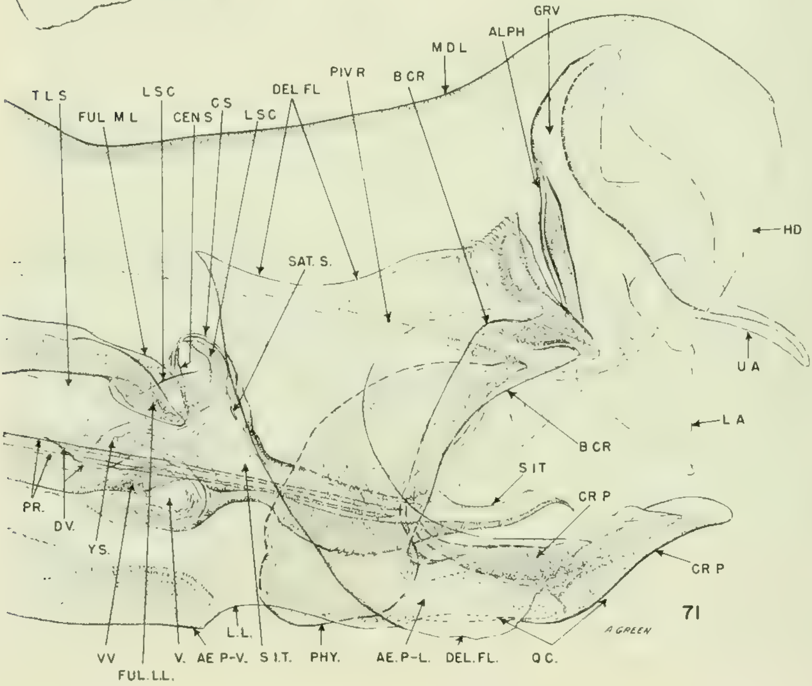


69

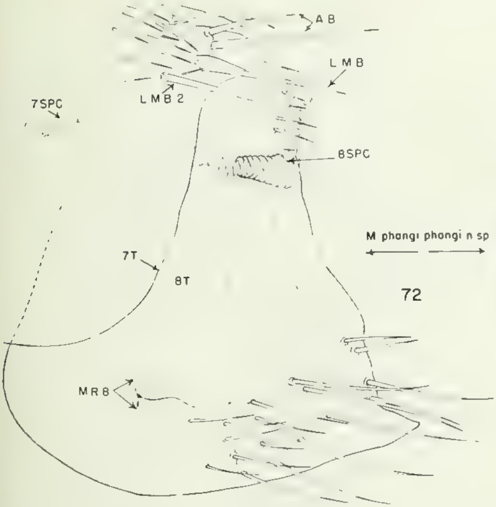


70

Medwayella phangi phangi n. sp.

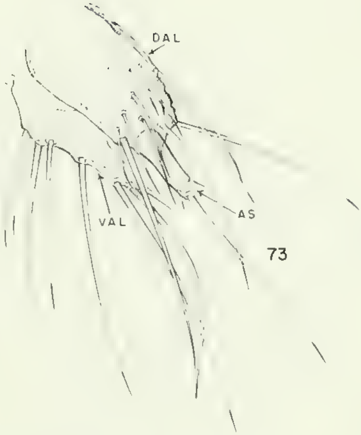

GRV
ALPH
M D L
PIV R
B CR
DEL FL
T L S
L S C
C S
FUL M L
CEN S
L S C
HD
SAT. S.
U A
L A
B CR
S IT
CR P
CR P
PR.
DV.
YS.
VV
FUL. L.L.
V.
AE P-V.
L.L.
S I.T.
PHY.
AE. P-L.
DEL. FL.
Q C.
A GREEN

71

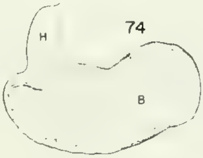

AB
LMB
LMB 2
7SPC
8SPC
7T
8T
MRB

M phongi phongi n sp

72

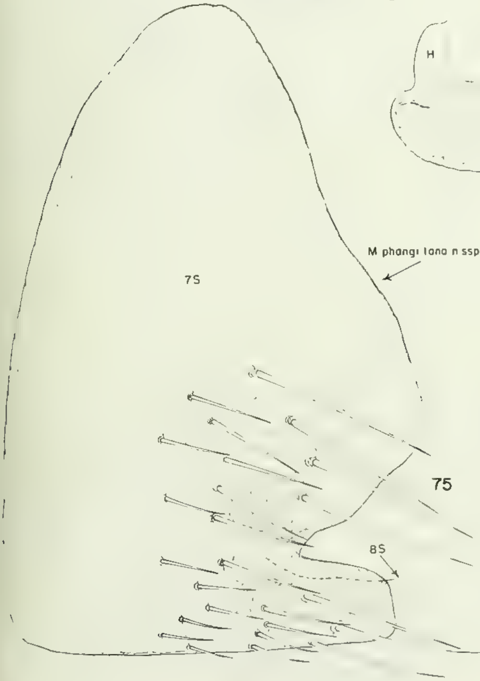


73



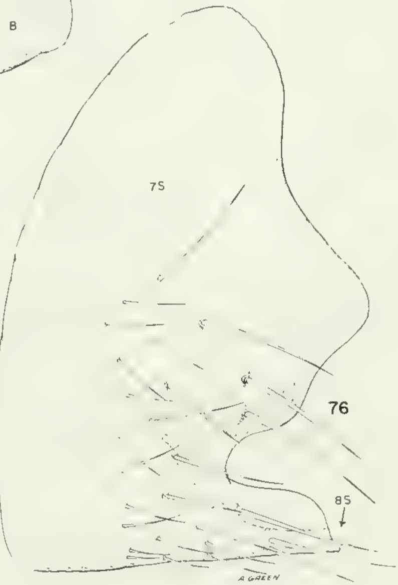
74

M phongi phongi n sp.

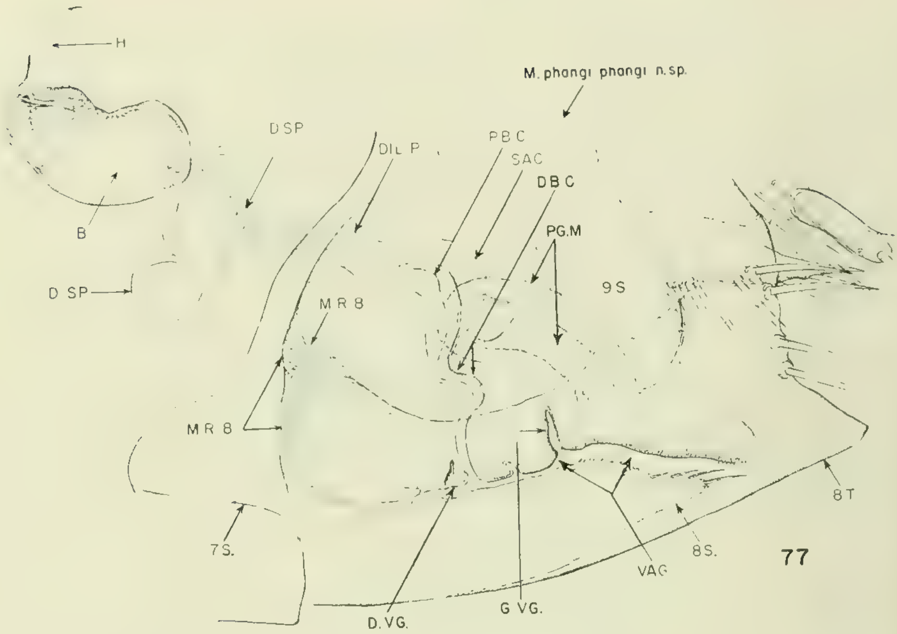


M phongi lana n ssp

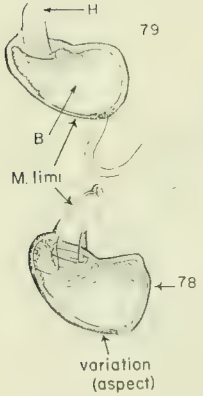
75

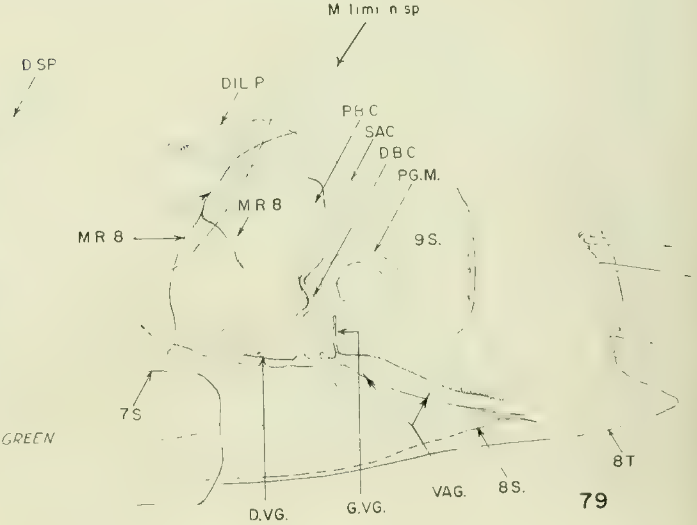

7S
8S
A GREEN

76


H
B
D SP
D SP
DIL P
M. phangi phangi n.sp.
PBC
SAC
DBC
PG.M
9S
MR 8
MR 8
8T
7S.
8S.
VAG
D.VG.
G VG.

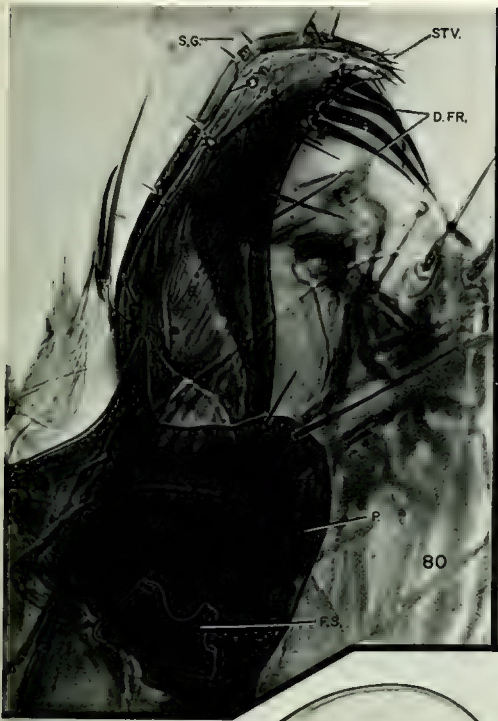
77

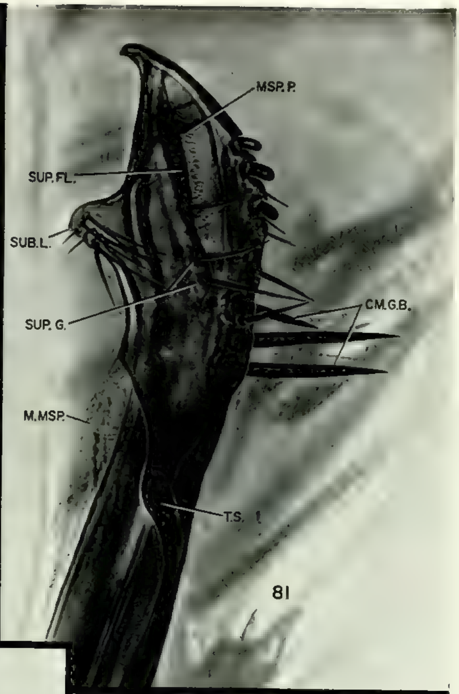

H
79
B
M. limi
78
variation
(aspect)

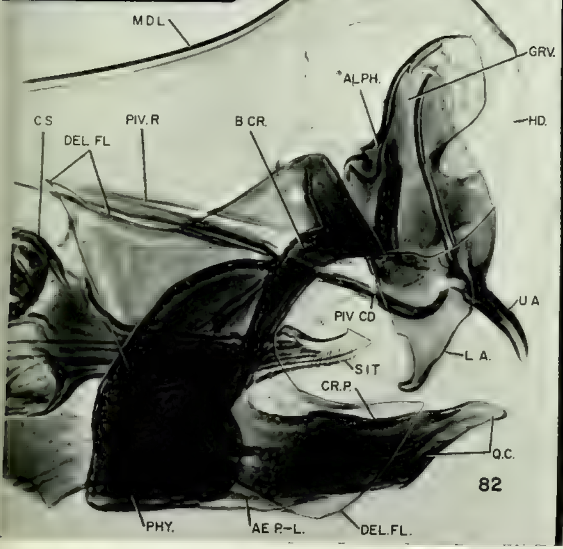

M limi n sp
D SP
DIL P
PBC
SAC
DBC
PG.M.
MR 8
MR 8
9S.
7S
8T
D.VG.
G.VG.
VAG.
8S.

79

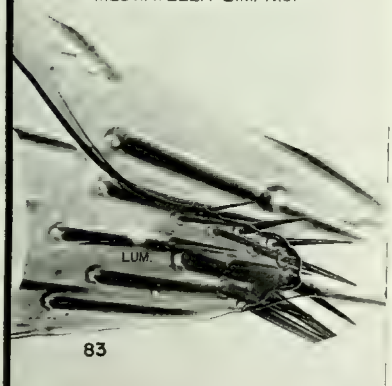
A GREEN


S.G.
STV.
D.FR.
P.
F.S.
80

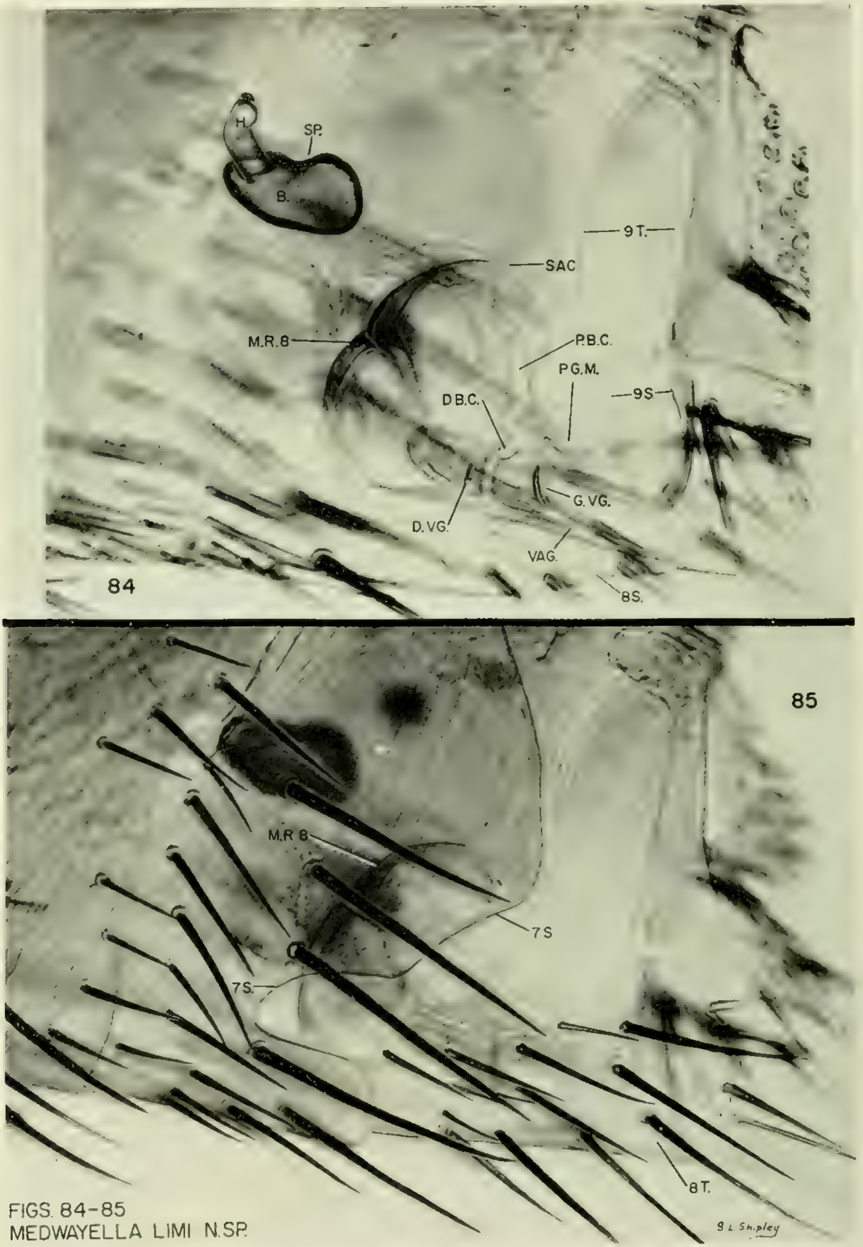

MSP.P.
SUP.FL.
SUB.L.
SUP.G.
CM.G.B.
M.MSP.
T.S.
81


MDL.
GRV.
ALPH.
C S
PIV. R
B CR.
HD.
DEL. FL
U A
PIV CD
L A.
SIT
CR.P.
Q.C.
82
PHY.
AE P.–L.
DEL.FL.

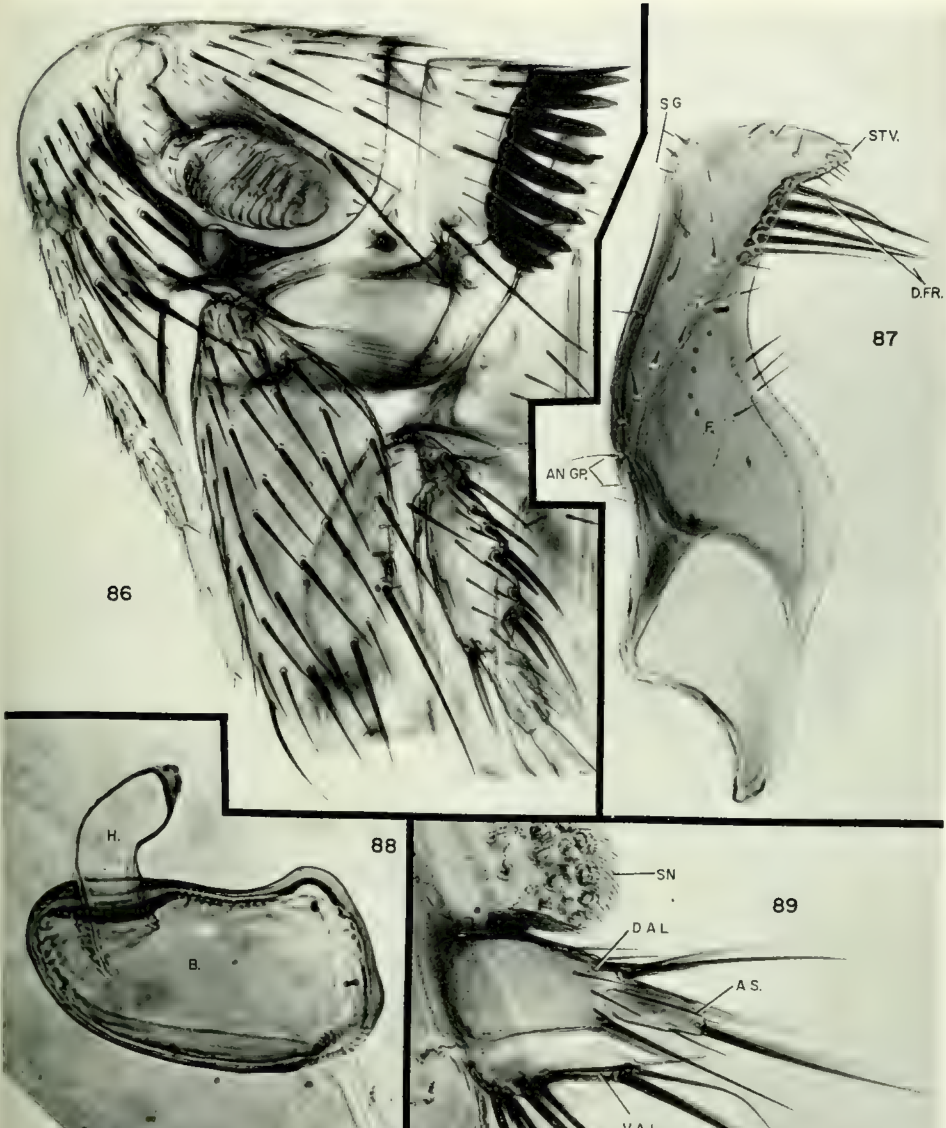
FIGS. 80–83
MEDWAYELLA LIMI N.SP



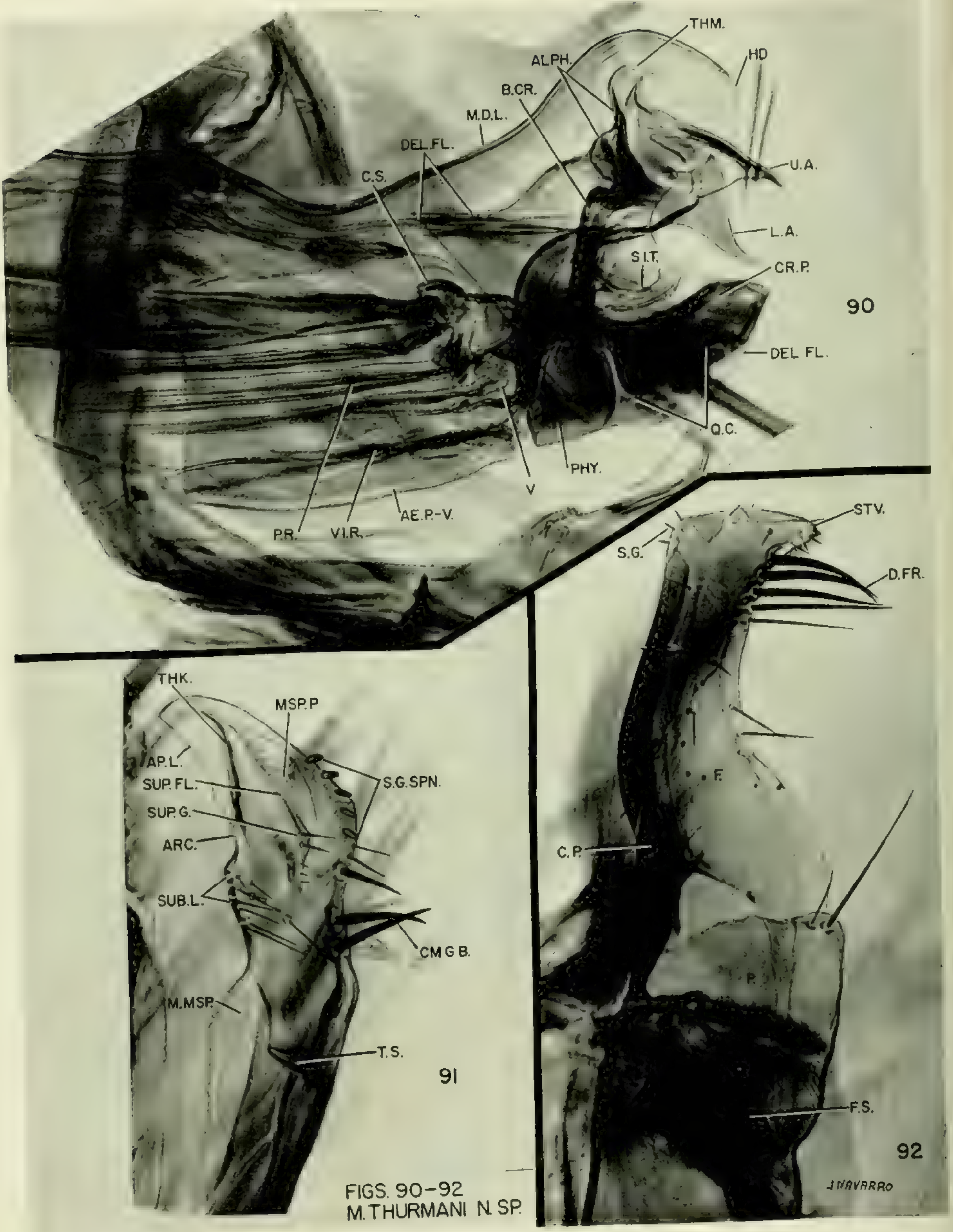
S L Shipley


H
SP.
B.
9T.
SAC
M.R.8
P.B.C.
P.G.M.
9S
D.B.C.
G.VG.
D.VG.
VAG.
8S.
84
85
M.R.8
7S
7S.
8T.
G L Shipley

FIGS. 84–85
MEDWAYELLA LIMI N.SP.


86
SG
STV.
D.FR.
87
F.
AN GP.
H.
88
B.
SN
89
DAL
AS.
VAL
J NAVARRO

FIGS. 86-89
M. THURMANI N.SP.


THM.
ALPH.
HD
B.CR.
M.D.L.
DEL.FL.
C.S.
U.A.
L.A.
S.I.T.
CR.P.
90
DEL.FL.
Q.C.
PHY.
V
AE.P.-V.
V.I.R.
P.R.
STV.
S.G.
D.FR.
F.
C.P.
P.
F.S.
92
J NAVARRO
THK.
MSP.P
AP.L.
S.G.SPN.
SUP.FL.
SUP.G.
ARC.
SUB.L.
CMGB.
M.MSP.
T.S.
91

FIGS. 90–92
M. THURMANI N. SP.

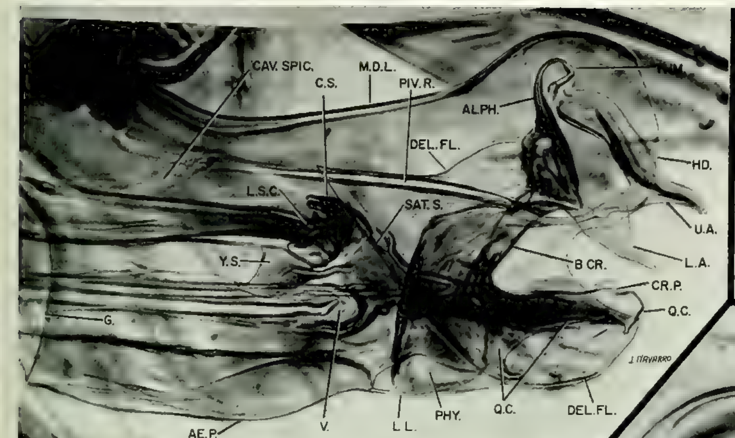

CAV. SPIC.
M.D.L.
C.S.
PIV.R.
THM.
ALPH.
DEL.FL.
HD.
L.S.C.
SAT.S.
U.A.
Y.S.
B CR.
L.A.
CR.P.
G.
Q.C.
J. NAVARRO
AE.P.
V.
L.L.
PHY.
Q.C.
DEL.FL.
93

FIG. 93
M. DRYADOSA N SP.

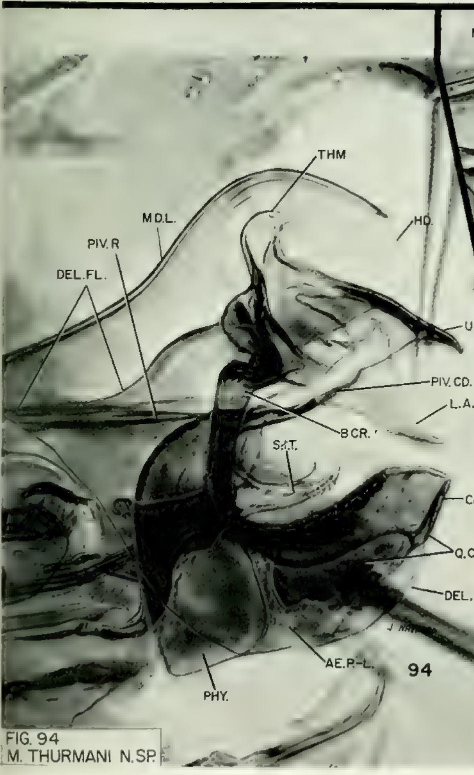
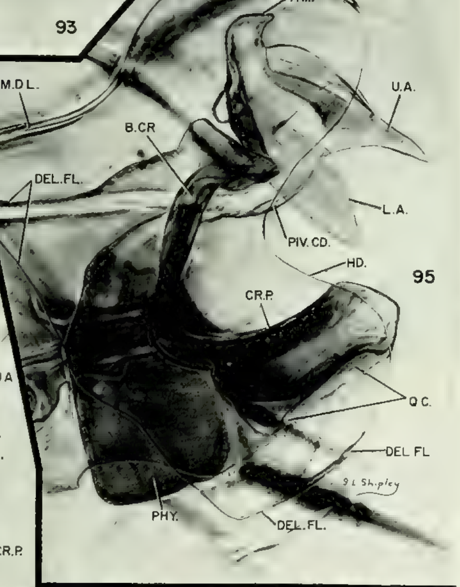
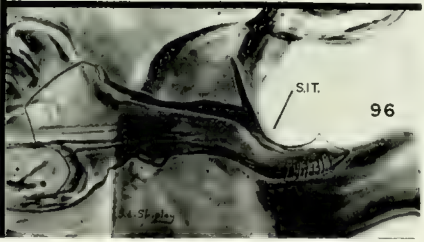
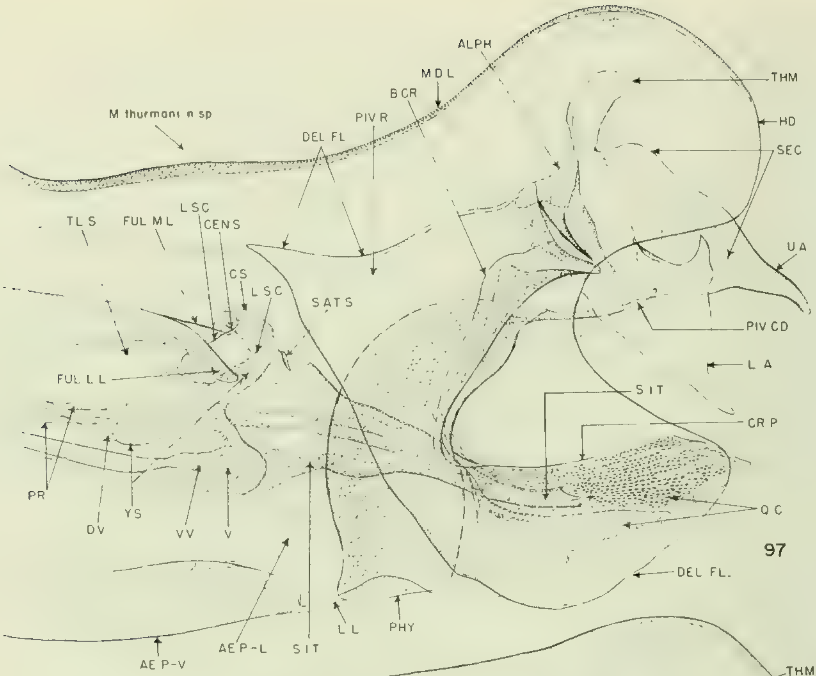

THM
M.D.L.
HD.
PIV.R
DEL.FL.
U.A
PIV.CD.
L.A.
B CR.
S.I.T.
CR.P.
Q.C.
DEL.FL.
J. NAVARRO
AE.P.-L.
94
PHY.

FIG. 94
M. THURMANI N.SP.

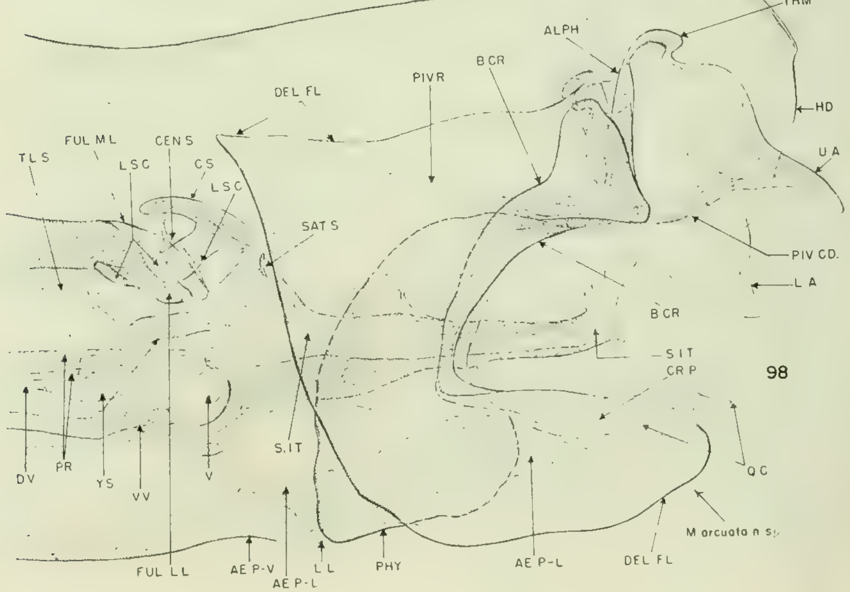
FIGS. 95-96
M. JAVANA
(JORDAN, 1933)


THM
M.D.L.
U.A.
B.CR
DEL.FL.
L.A.
PIV.CD.
HD.
95
CR.P.
Q.C.
DEL.FL
G L Shipley
PHY.
DEL.FL.

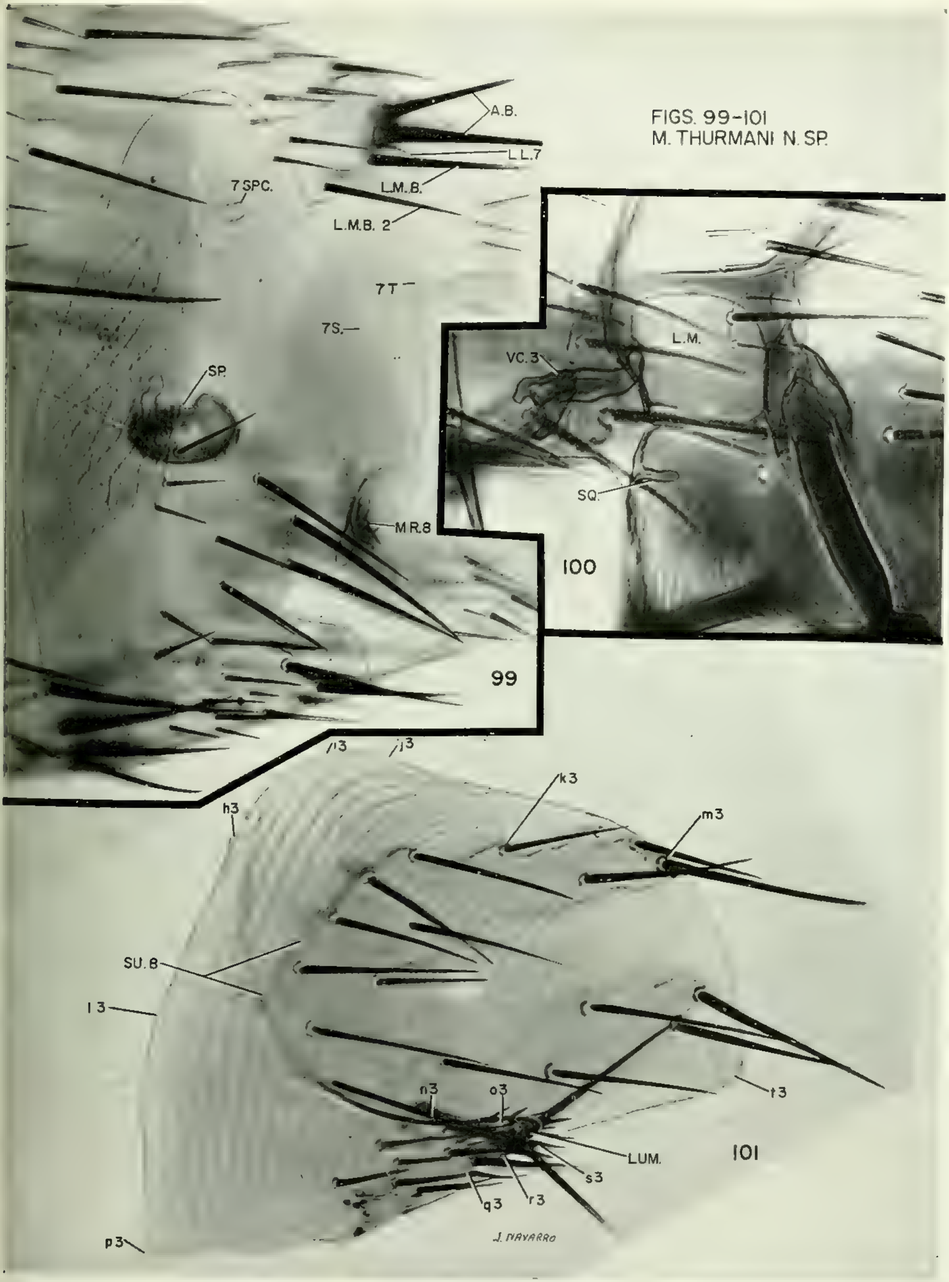

S.I.T.
96
G.L. Shipley


M thurmani n sp
ALPH
M D L
B CR
PIV R
DEL FL
THM
HD
SEC
UA
PIV CD
L A
S I T
CR P
Q C
DEL FL.
TLS
FUL ML
L SC
CEN S
C S
L SC
SAT S
FUL L L
PR
DV
YS
VV
V
AE P-V
AE P-L
S I T
L L
PHY

97


THM
ALPH
B CR
PIVR
DEL FL
HD
UA
TLS
FUL ML
CEN S
L SC
C S
L S C
SAT S
PIV CD.
L A
B CR
S I T
CR P
Q C
DV
PR
YS
VV
V
S.IT
FUL L L
AE P-V
AE P-L
L L
PHY
AE P-L
DEL FL
M arcuata n sp

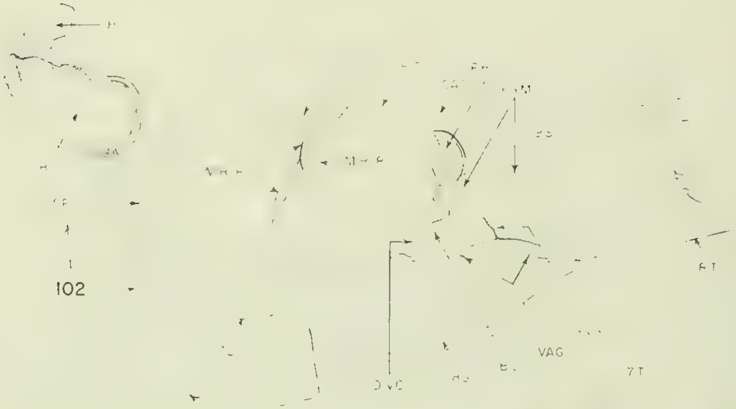
98



FIGS. 99-101
M. THURMANI N. SP.

A.B.
L.L.7
L.M.B.
L.M.B. 2
7 SPC.
7T
7S.
SP.
M.R.8
99
VC.3
L.M.
SQ.
100
i3
j3
k3
m3
h3
SU.8
l 3
t3
n3
o3
LUM.
s3
r3
q3
p3
101
J. NAVARRO

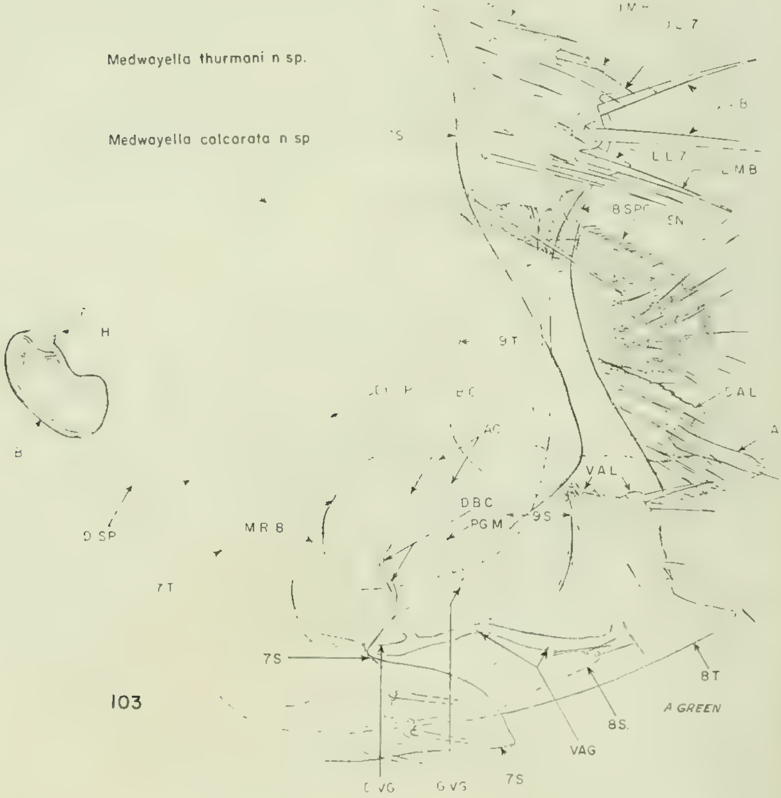
102

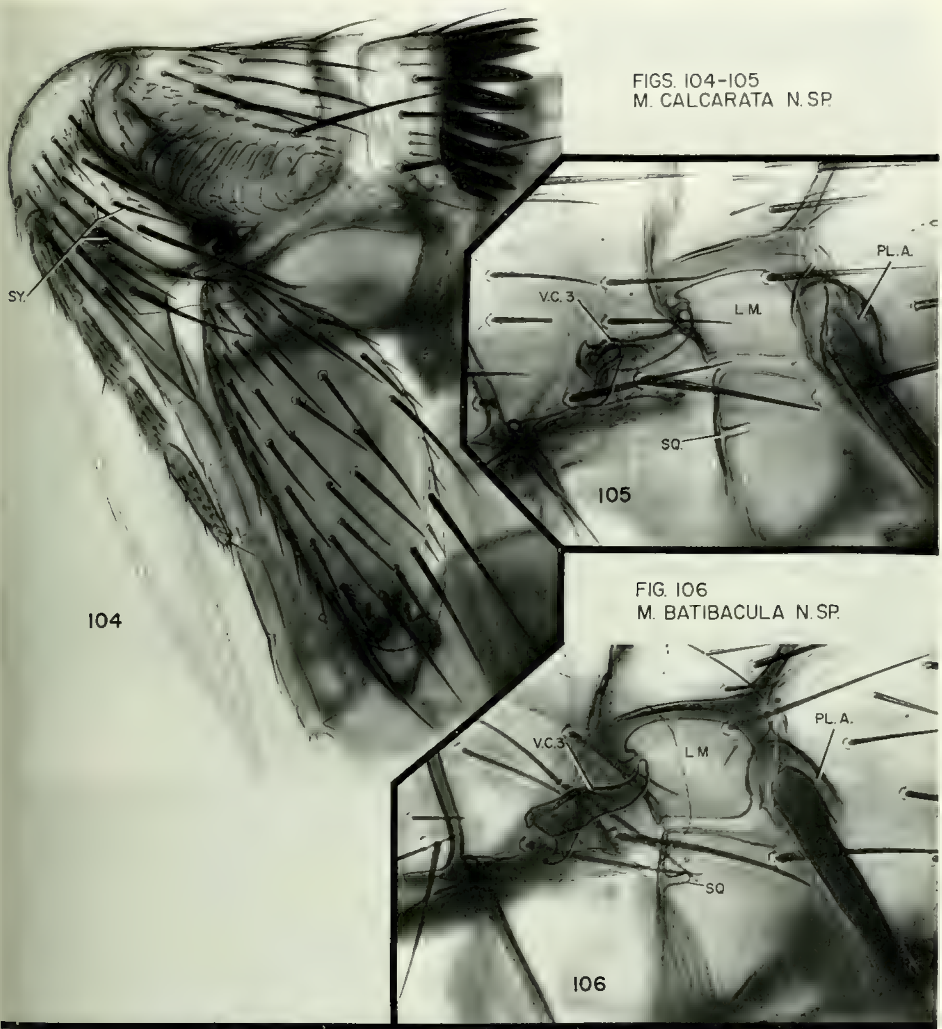

VAG
7T
6T
DVC
SS
MRP

Medwayella thurmani n sp.

Medwayella calcarata n sp

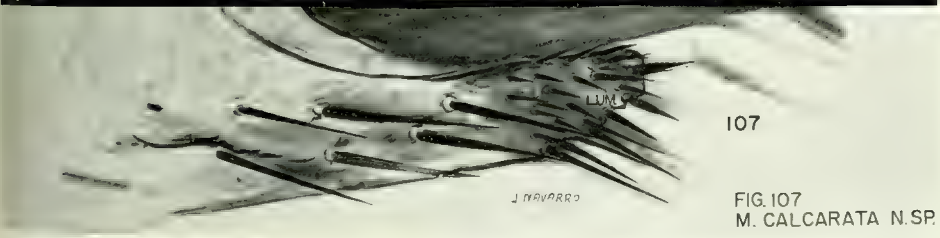
103


JMP
LL7
LMB
8SPC
SN
9T
SAL
AS
H
B
AC
VAL
DBC
PGM
9S
DSP
MRB
7T
7S
8T
8S
VAG
DVG
GVG
7S
A GREEN


SY.
104
V.C. 3
L.M.
PL.A.
SQ.
105
V.C.3
L M
PL. A.
SQ
106

FIGS. 104–105
M. CALCARATA N. SP.

FIG. 106
M. BATIBACULA N. SP.



J NAVARRO

FIG. 107
M. CALCARATA N. SP.

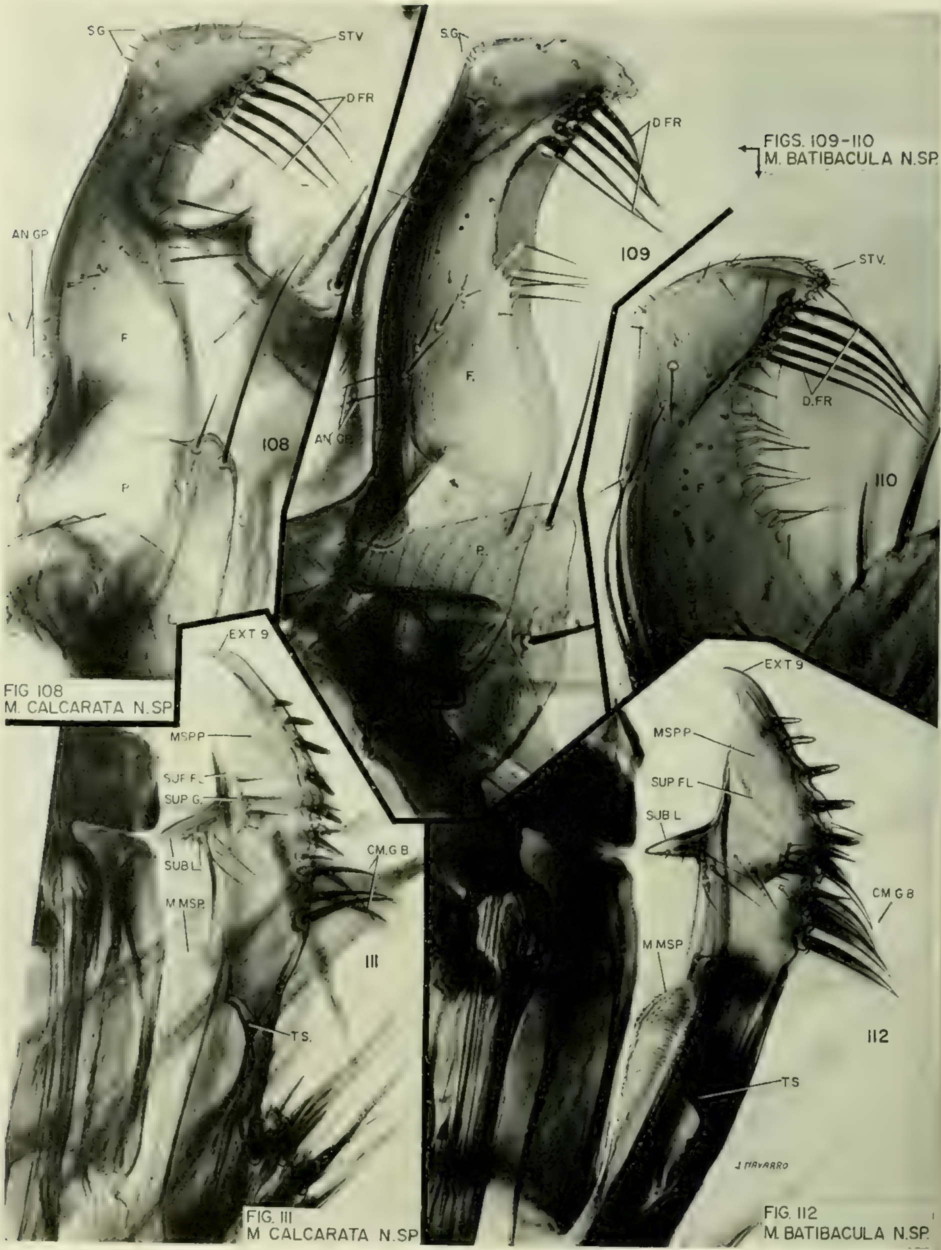

SG
STV
D FR
AN GP
F
P
108
S.G
D FR
109
F.
AN GP
P.
STV.
D.FR
F
110
EXT 9
MSPP
SUP FL
SUP G.
SUB L
M MSP
CM.G B
TS.
111
EXT 9
MSPP
SUP FL
SUB L
M MSP
CM G B
112
TS
J NAVARRO

FIG 108
M. CALCARATA N.SP

FIGS. 109–110
M. BATIBACULA N.SP.

FIG. 111
M CALCARATA N.SP

FIG. 112
M. BATIBACULA N.SP.

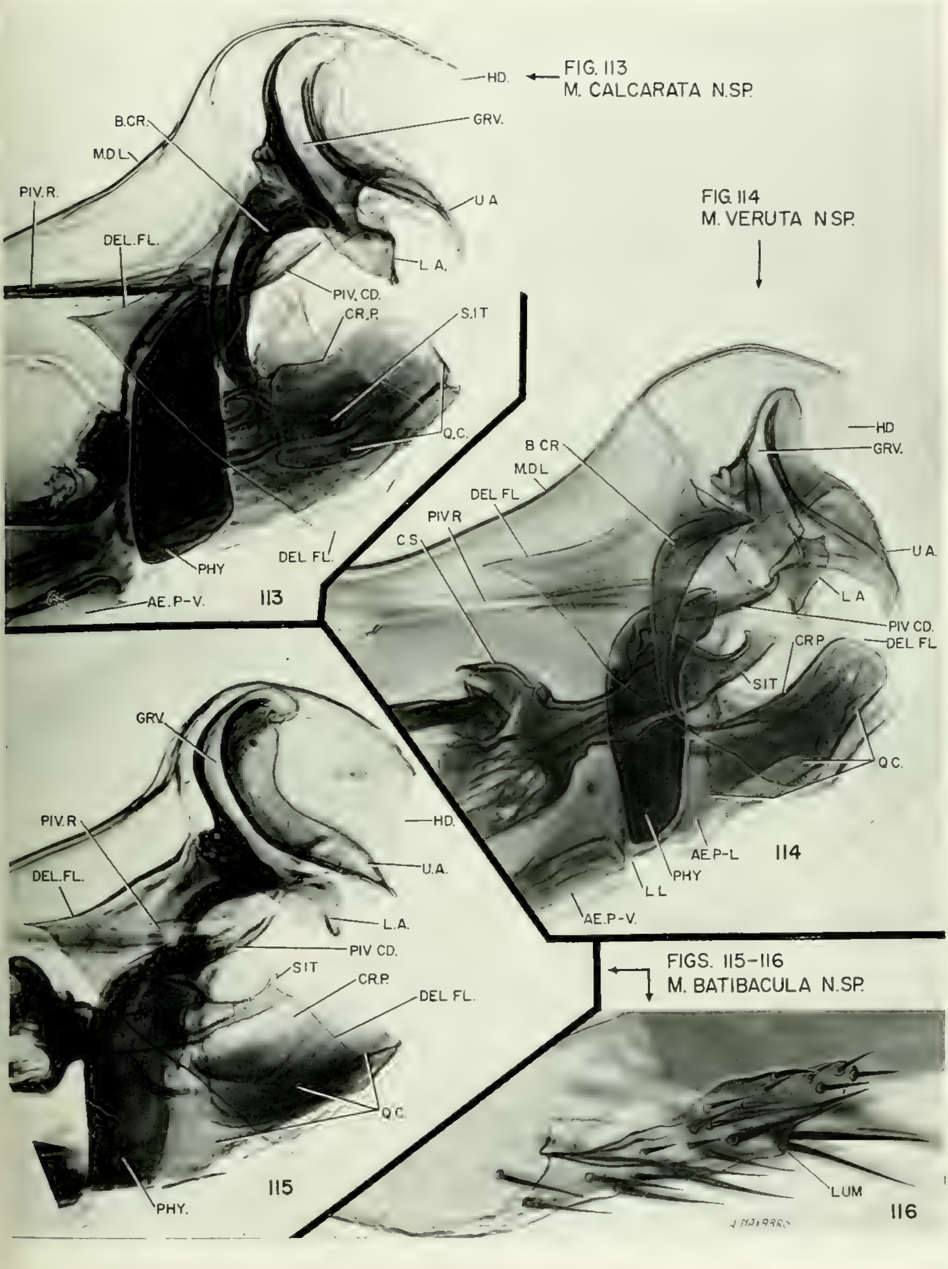
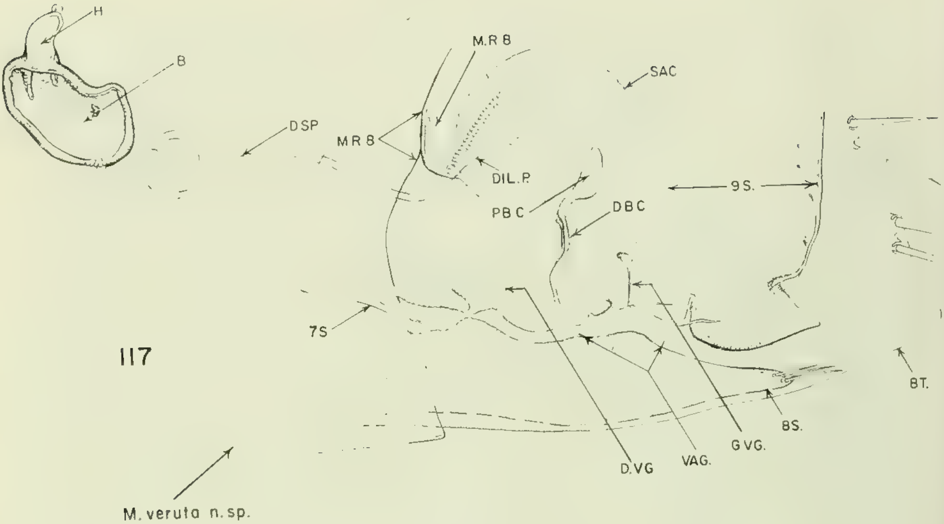

HD.
GRV.
B.CR.
M.D.L.
PIV.R.
U.A.
DEL.FL.
L.A.
PIV.CD.
CR.P.
S.I.T
Q.C.
PHY
DEL.FL.
AE.P-V.
113
HD
GRV.
B CR
M.D.L
DEL FL
PIV R
C S
U.A.
L A
PIV CD.
CR P
DEL FL
S.I.T
Q.C.
AE.P-L
114
PHY
L L
AE.P-V.
GRV.
PIV.R
HD.
U.A.
DEL.FL.
L.A.
PIV CD.
S.I.T
CR.P.
DEL FL.
Q.C.
115
PHY.
LUM
116

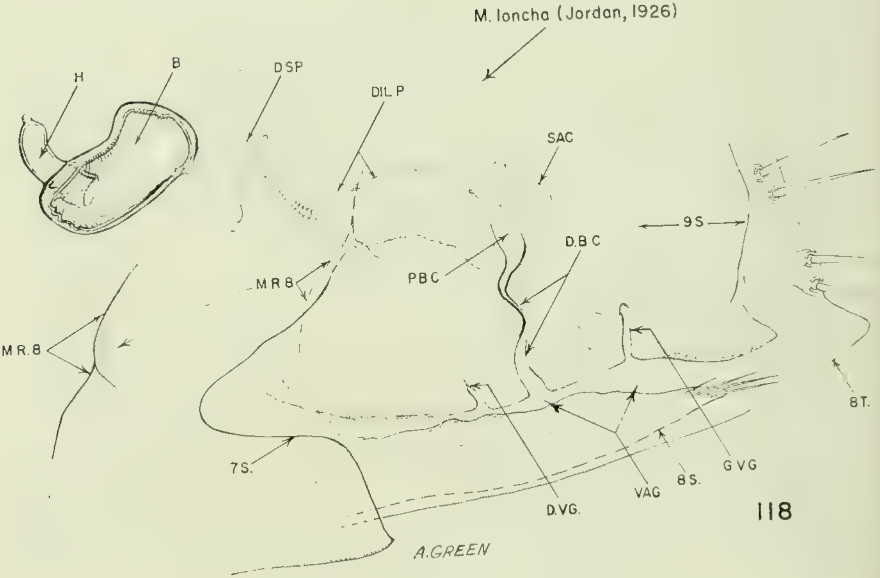
FIG. 113
M. CALCARATA N.SP.

FIG. 114
M. VERUTA N.SP.

FIGS. 115–116
M. BATIBACULA N.SP.

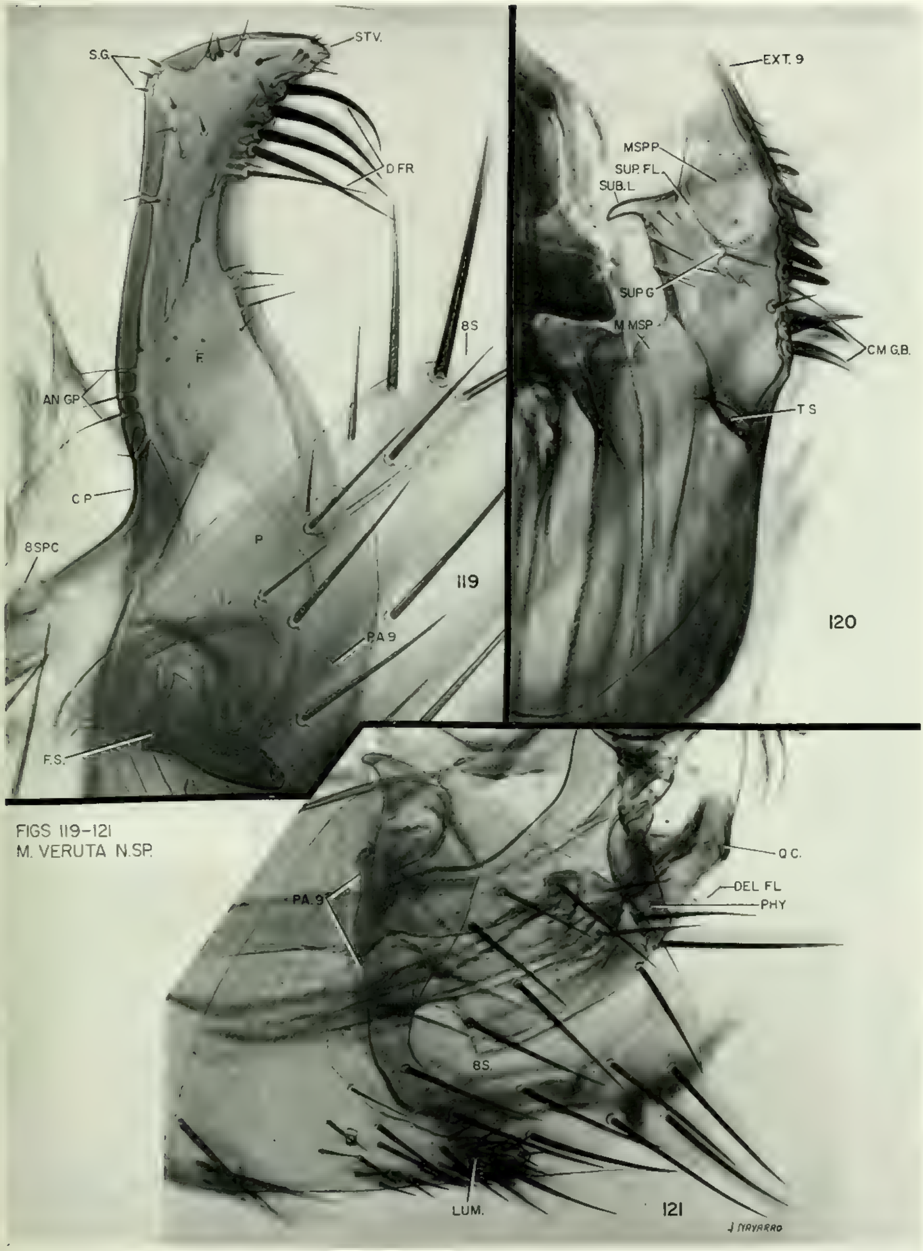

H
B
DSP
M.R 8
MR 8
SAC
DIL.P.
PBC
DBC
9S.
7S
8T.
8S.
GVG.
VAG.
D.VG
M. veruta n.sp.

117

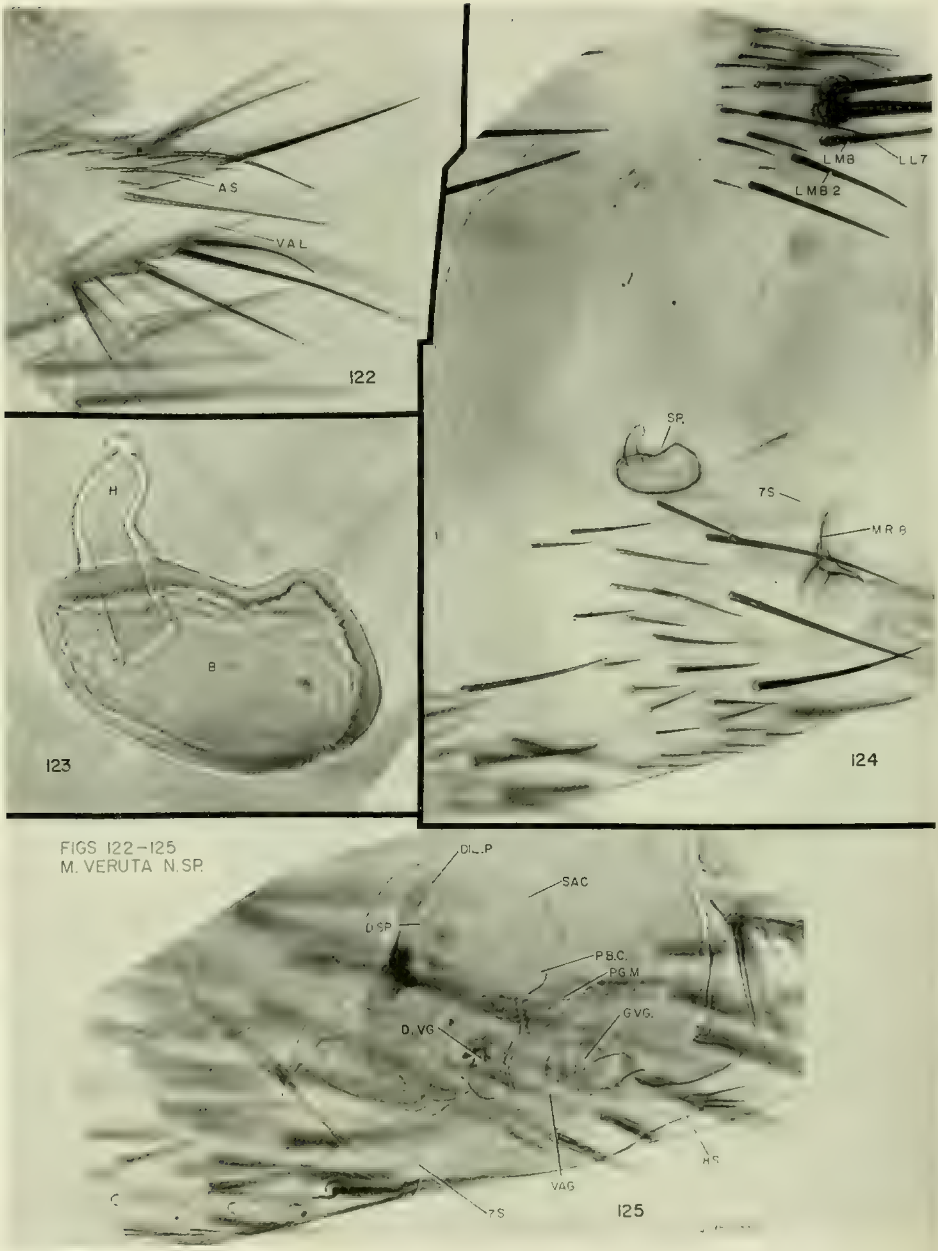

M. loncha (Jordan, 1926)
H
B
DSP
DIL P
SAC
9S
D.B C
PBC
MR 8
MR.8
8T.
7S.
VAG
8S.
GVG
D.VG.

118

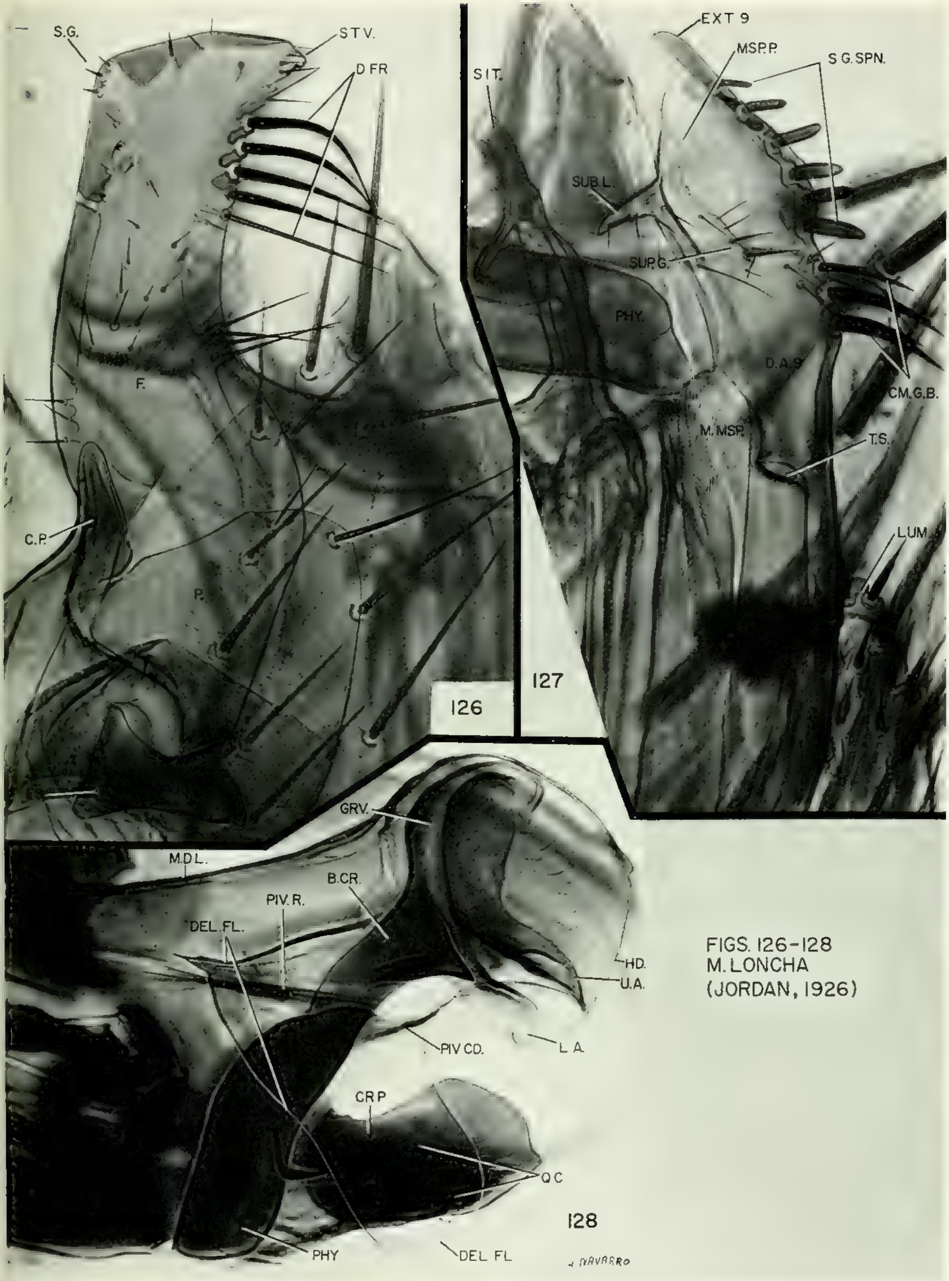
A.GREEN


S.G.
STV.
D.FR
F
AN GP
C P
P
8SPC
8S
P.A.9
F.S.
119
EXT. 9
MSPP
SUP. FL.
SUB.L
SUP. G
M. MSP
CM G.B.
T S
120
Q C.
DEL FL
PHY
PA.9
8S.
LUM.
121
J NAVARRO

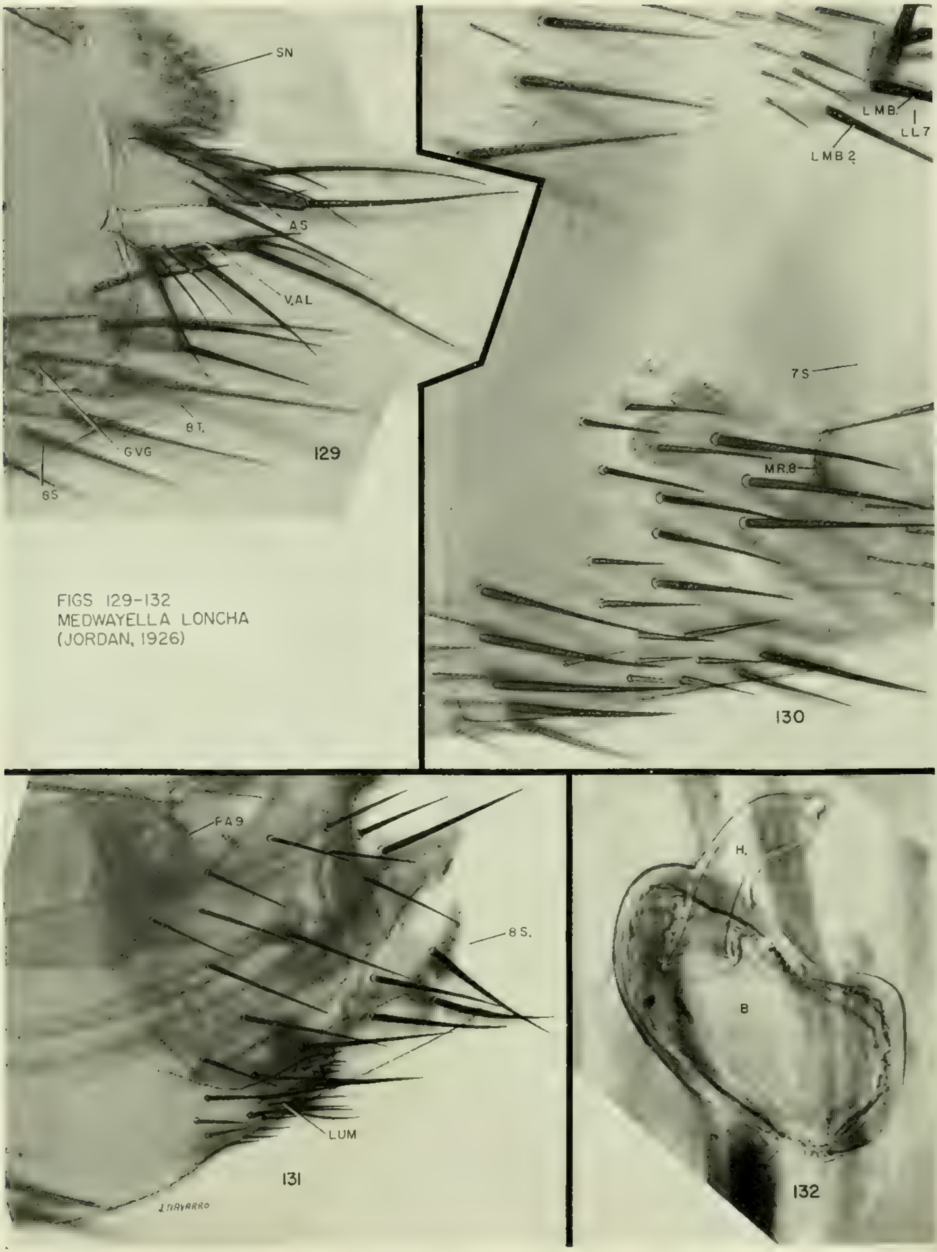
FIGS 119–121
M. VERUTA N.SP.


AS
VAL
122
H
B
123
LMB
LL7
LMB 2
SP.
7S
MR 8
124
DIL.P
SAC
DSP
PB.C.
PG.M
GVG.
D.VG
HS
VAG
7S
125

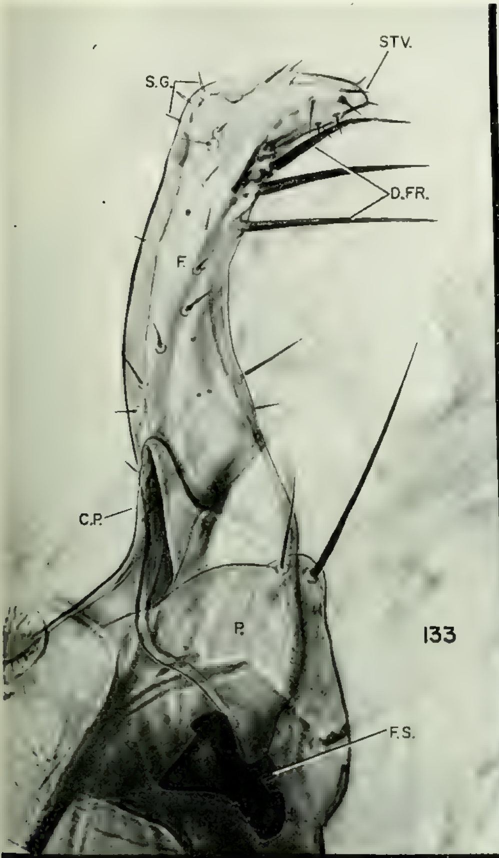
FIGS 122–125
M. VERUTA N.SP.

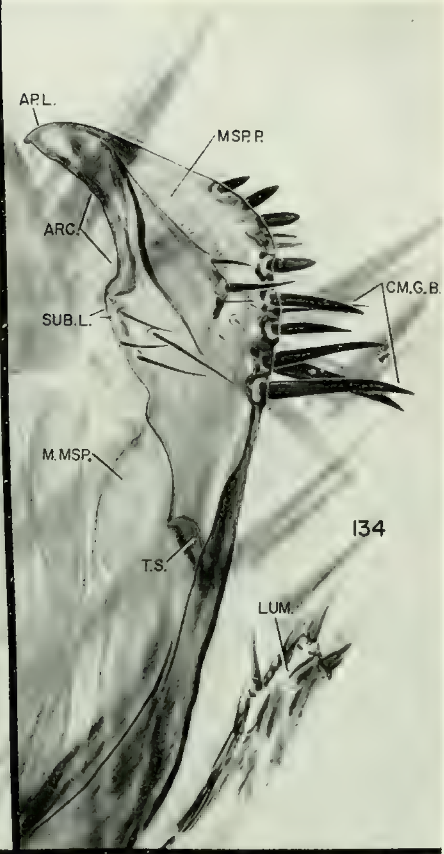

S.G.
STV.
D FR
F.
C.P.
P.
F.S.
126
EXT 9
MSP.P.
S G. SPN.
SIT.
SUB.L.
SUP.G.
PHY.
D.A.9
CM.G.B.
M. MSP.
T.S.
LUM.
127
GRV.
M.D.L.
B.CR.
PIV. R.
DEL. FL.
HD.
U.A.
PIV CD.
L A.
CRP
O C
128
PHY
DEL FL
J NAVARRO

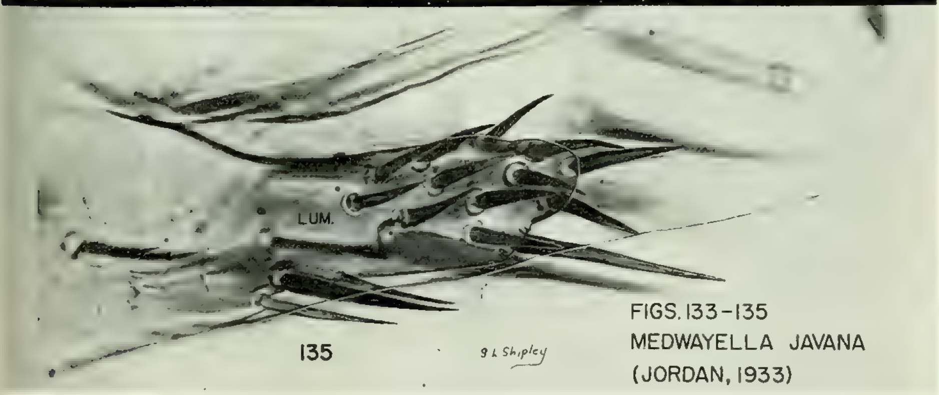
FIGS. 126–128
M. LONCHA
(JORDAN, 1926)


SN
AS
V.AL
8T.
GVG
8S
129
LMB.
LL7
LMB 2
7S
MR.8
130
FA9
8S.
LUM
131
I. NAVARRO
H.
B
132

FIGS 129–132
MEDWAYELLA LONCHA
(JORDAN, 1926)

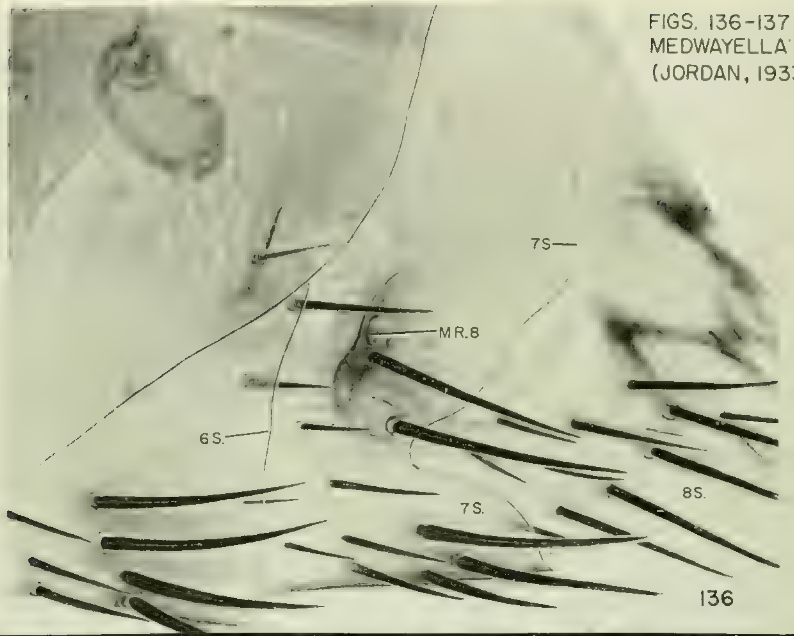

STV.
S.G.
D.FR.
F.
C.P.
P.
F.S.
133


AP.L.
MSP.P.
ARC.
CM.G.B.
SUB.L.
M.MSP.
T.S.
LUM.
134

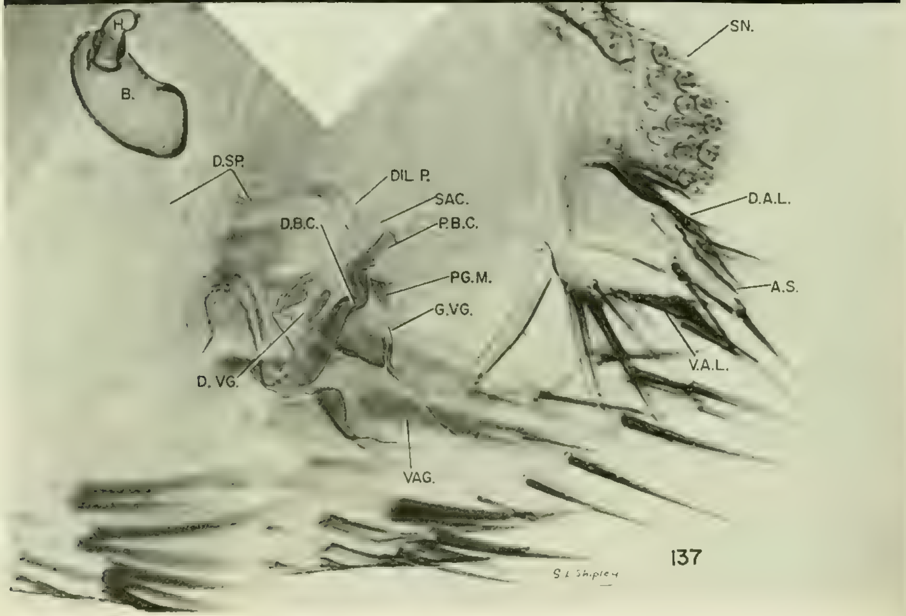

LUM.
135
G L Shipley

FIGS. 133–135
MEDWAYELLA JAVANA
(JORDAN, 1933)

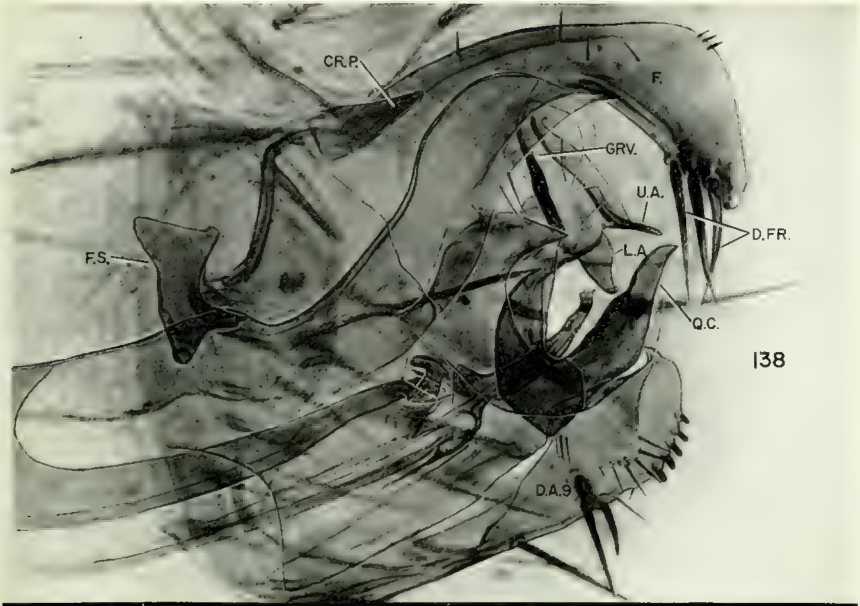
FIGS. 136–137
MEDWAYELLA JAVANA
(JORDAN, 1933)


7S
MR.8
6S.
7S.
8S.

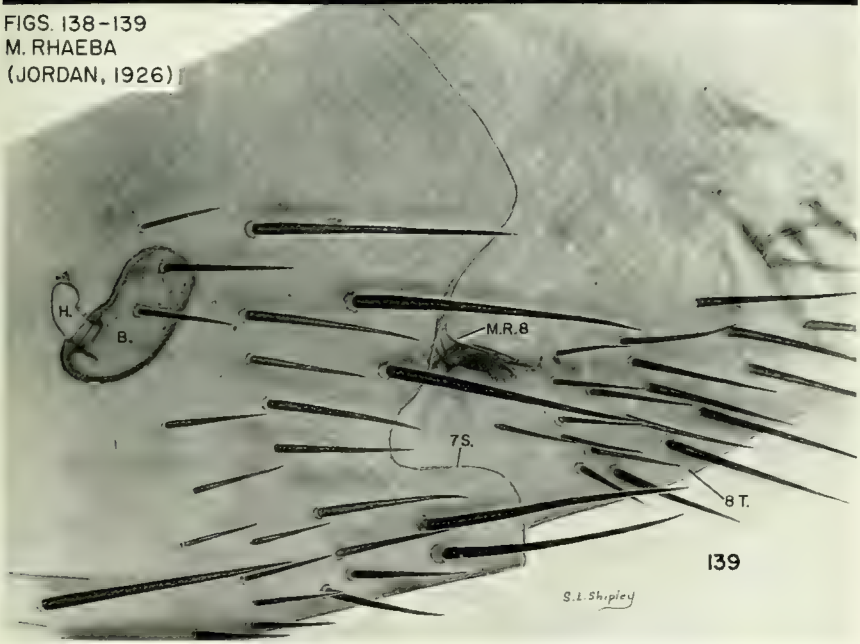
136

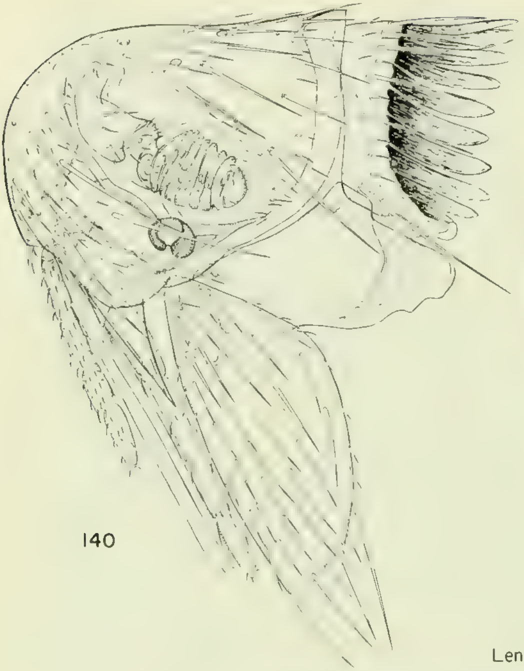

SN.
H
B.
D.SP.
DIL. P.
SAC.
D.B.C.
P.B.C.
PG.M.
G.VG.
D. VG.
D.A.L.
A.S.
V.A.L.
VAG.
S L Shipley

137

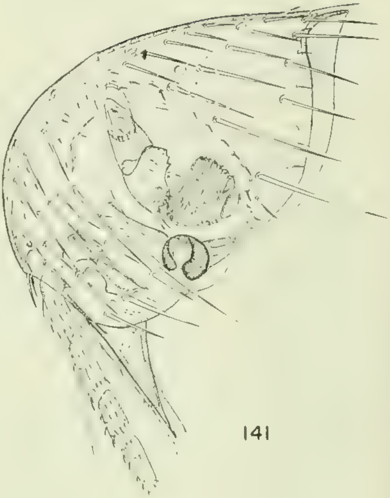

CR.P.
F.
GRV.
U.A.
D.FR.
F.S.
L.A.
Q.C.
138
D.A.9

FIGS. 138–139
M. RHAEBA
(JORDAN, 1926)


H.
B.
M.R.8
7S.
8 T.
139
S.L. Shipley

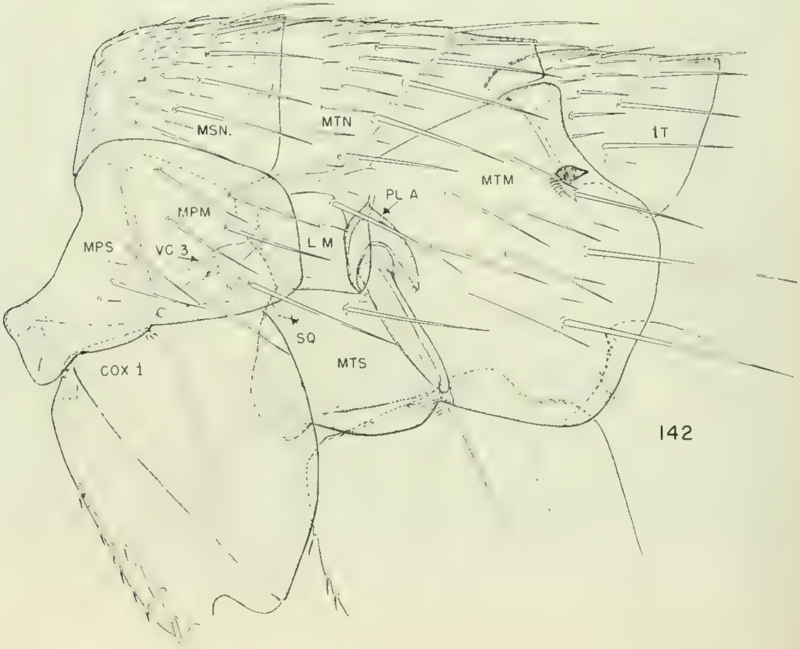


140

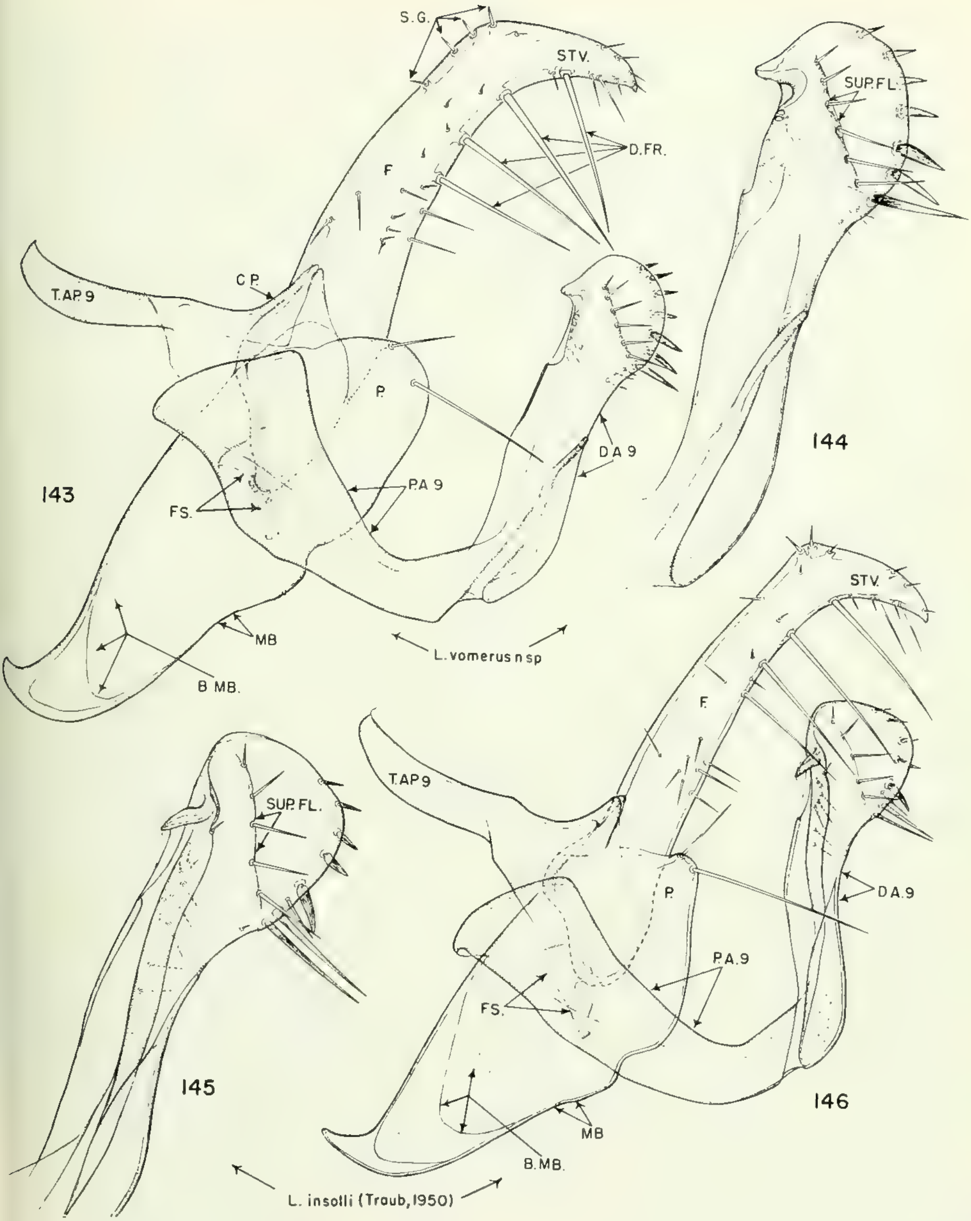


141

Lentistivalius vomerus n sp.


MSN.
MTN
1T
MTM
PL A
MPM
L M
MPS
VC 3
SQ
MTS
COX 1

142


S.G.
STV.
D.FR.
F
T.AP. 9
C.P.
P.
D.A 9
P.A 9
F.S.
MB
B MB.
SUP.FL.
T.AP 9
STV.
F
P.
D.A.9
P.A.9
F.S.
MB
B.MB.
SUP.FL.

143

144

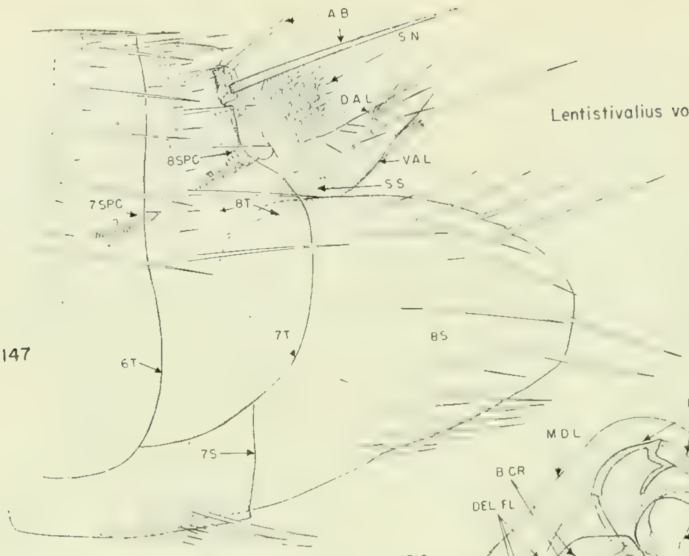
L. vomerus n sp

145

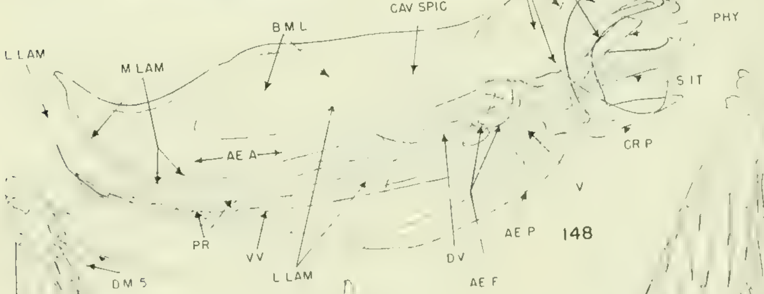
146

L. insolli (Traub, 1950)

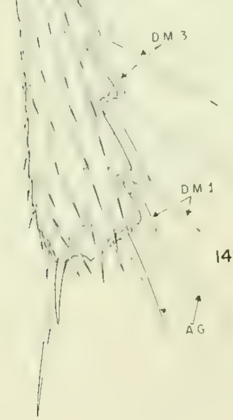
Lentistivalius vomerus n.sp.


AB
SN
DAL
8SPC
VAL
SS
7SPC
8T
7T
8S
6T
7S

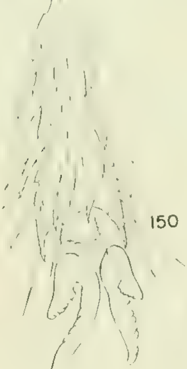
147


FSC
MDL
BCR
DEL FL
HD
PHY
CAV SPIC
BML
L LAM
M LAM
AE A
SIT
CR P
V
PR
VV
L LAM
DV
AE P
AE F

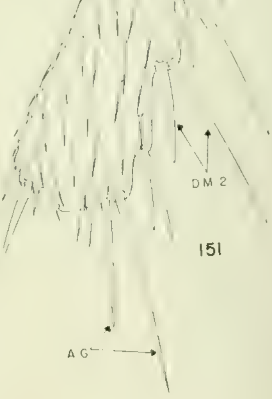
148


DM 5
DM 3
DM 1
AG

149

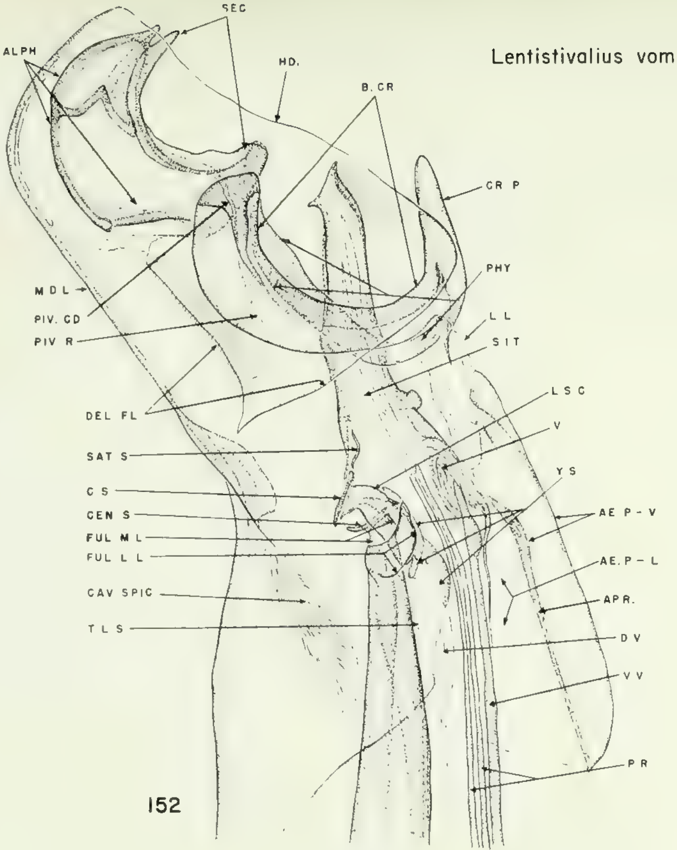


150


DM 6
DM 4
DM 2
AG

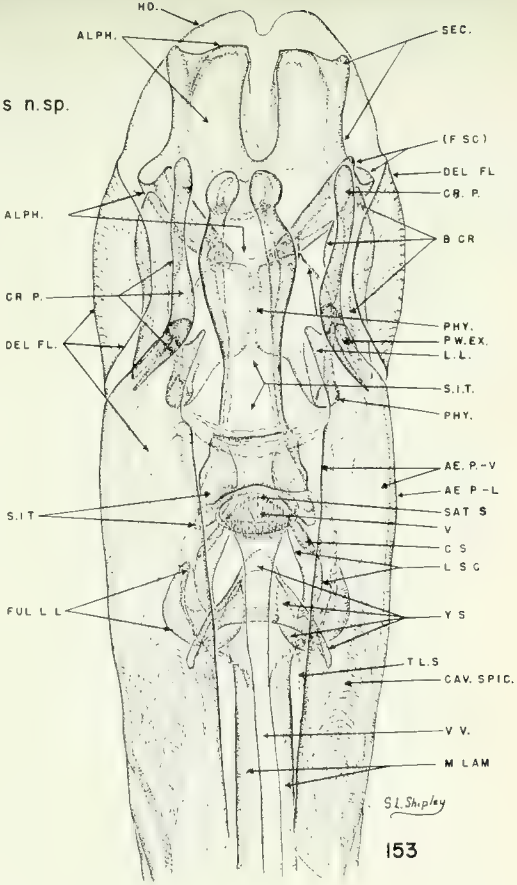
151

Lentistivalius vomerus n.sp.


ALPH
SEC
HD.
B. CR
CR P
PHY
L L
S I T
M D L
PIV. CD
PIV R
DEL FL
L S C
V
Y S
SAT S
C S
CEN S
FUL M L
FUL L L
AE P - V
AE. P - L
APR.
CAV SPIC
T L S
D V
V V
P R

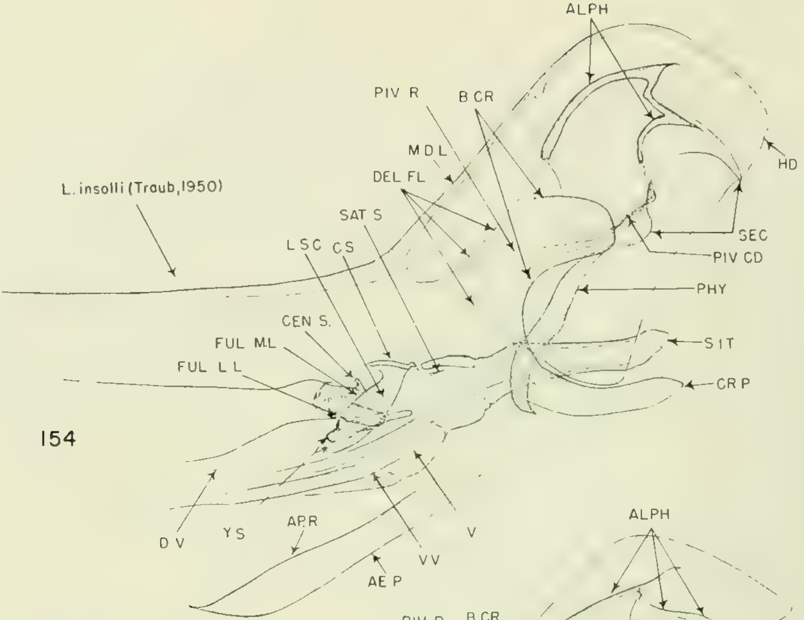
152

lateral aspect

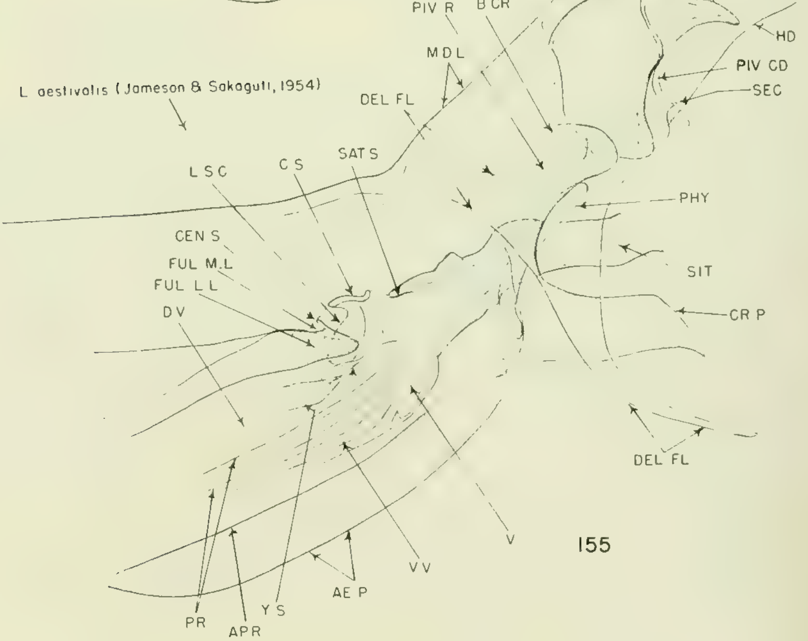

HD.
ALPH.
SEC.
(F SC)
DEL FL
CR. P.
ALPH.
B CR
CR P.
DEL FL.
PHY.
P.W. EX.
L.L.
S.I.T.
PHY.
AE. P.-V
AE P -L
SAT S
S.I T
V
C S
L S C
FUL L L
Y S
T L.S
CAV. SPIC.
V V.
M LAM
S.L. Shipley

153

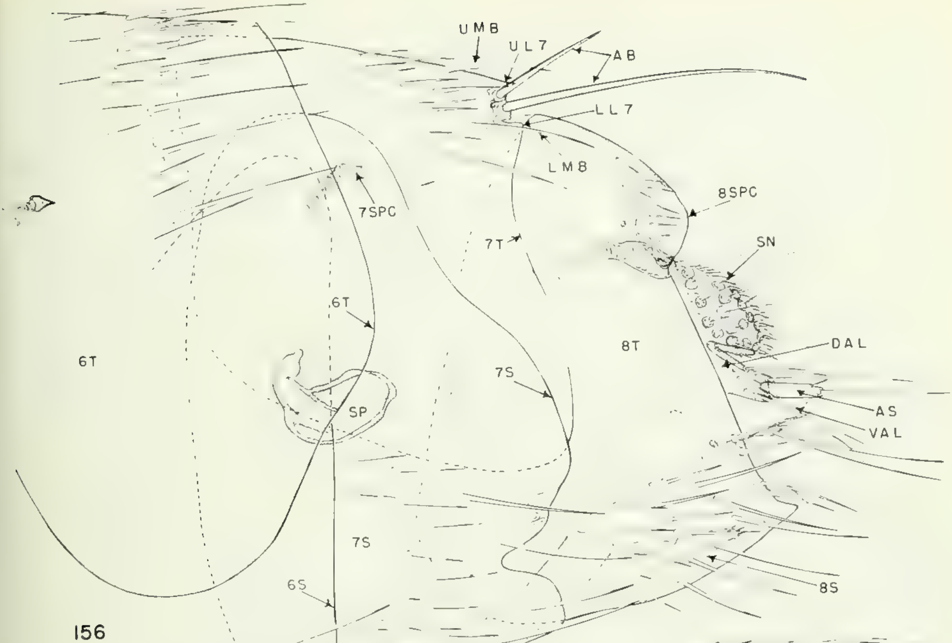
ventral aspect


ALPH
PIV R
B CR
M D L
HD
L. insolli (Traub,1950)
DEL FL
SAT S
SEC
L S C
C S
PIV CD
PHY
CEN S.
FUL M.L
S I T
FUL L L
CR P
D V
Y S
AP R
V
V V
AE P

154

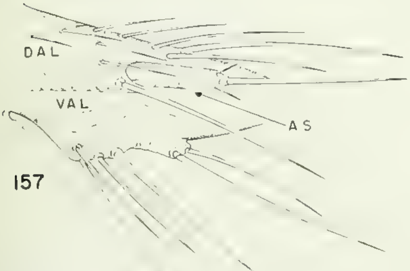

ALPH
PIV R
B CR
HD
M D L
PIV CD
L aestivalis (Jameson & Sakaguti, 1954)
DEL FL
SEC
SAT S
L S C
C S
PHY
CEN S
FUL M.L
S I T
FUL L L
D V
CR P
DEL FL
V
V V
AE P
PR
APR
Y S

155

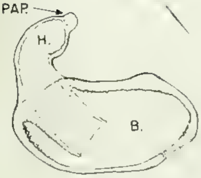

UMB
UL7
AB
LL7
LMB
7SPC
8SPC
SN
7T
6T
6T
8T
DAL
7S
SP
AS
VAL
7S
6S
8S

156

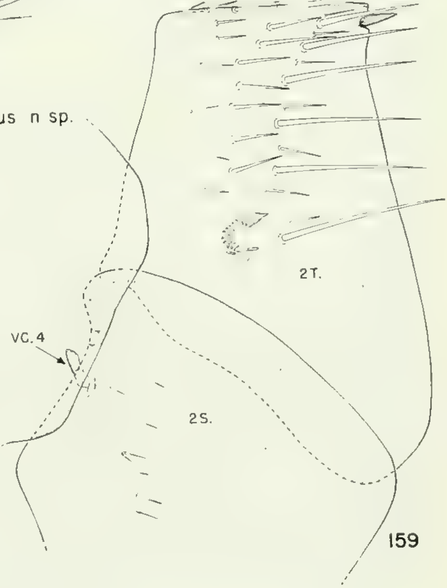
Lentistivalius vomerus n sp.



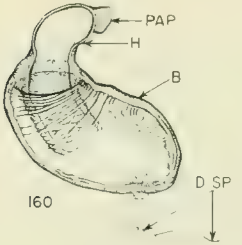
157



158

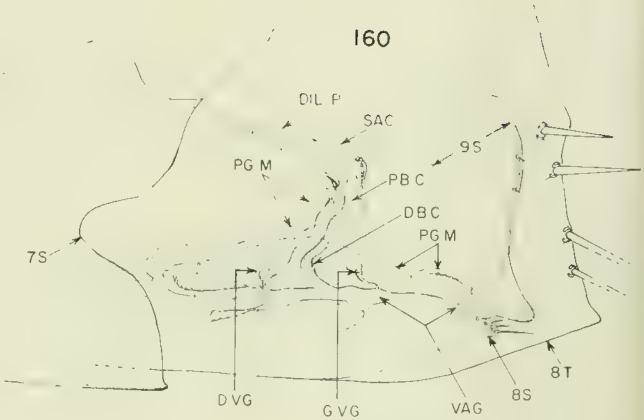


159

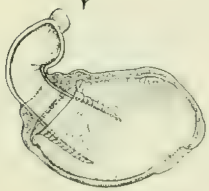


160

L. vomerus n. sp.


DIL P
SAC
9S
PG M
PB C
DBC
PG M
7S
DVG
GVG
VAG
8S
8T

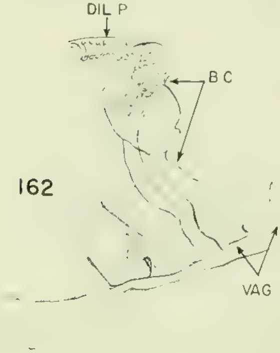
160



161

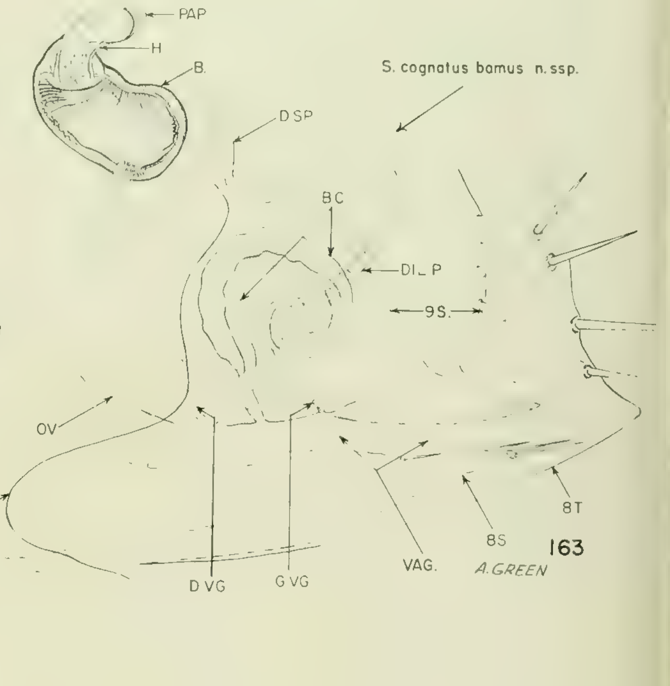
variation
(aspect)

S. phoberus Jordan & Rothschild, 1922

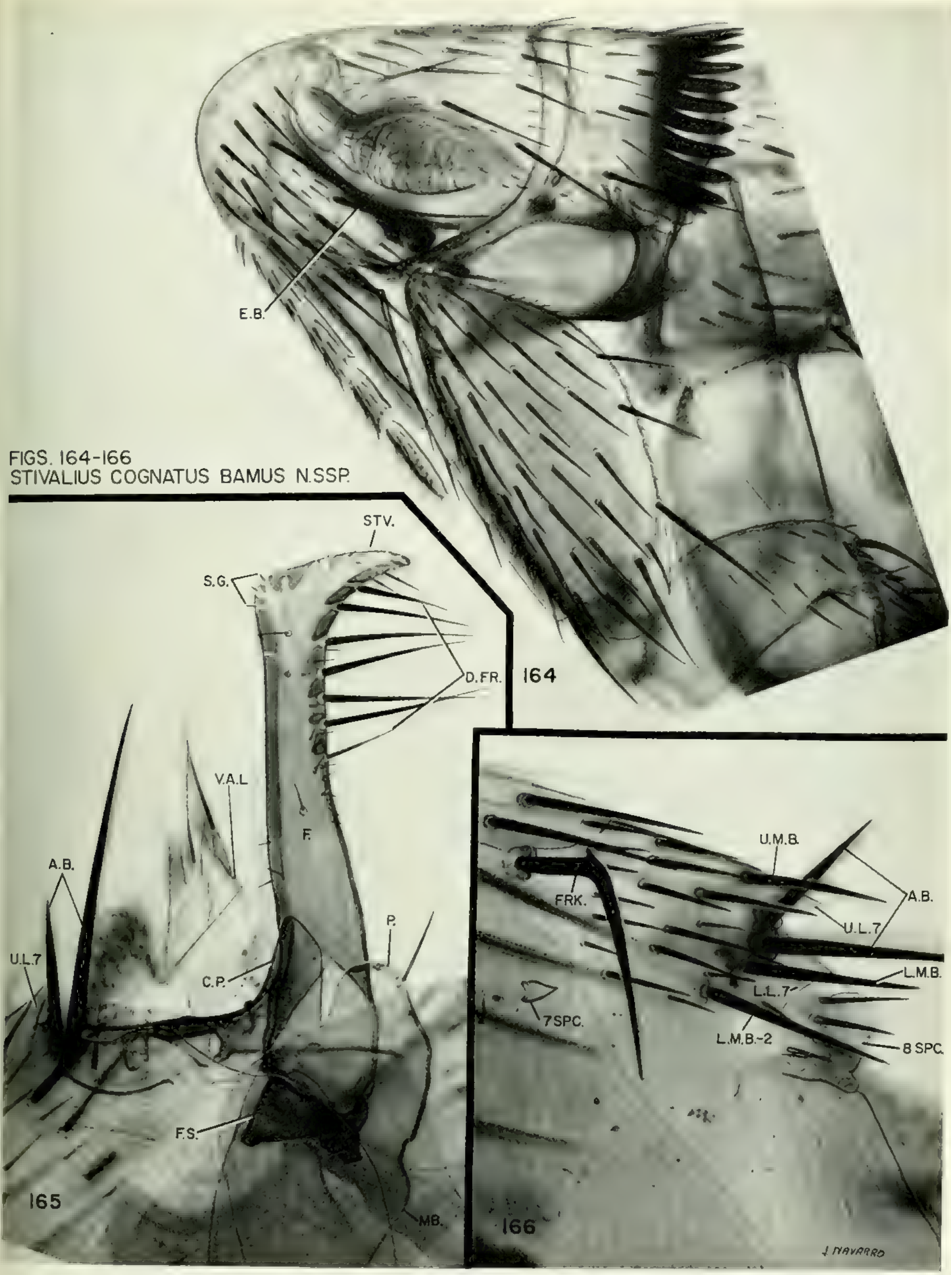


162

S. cognatus bamus n. ssp.

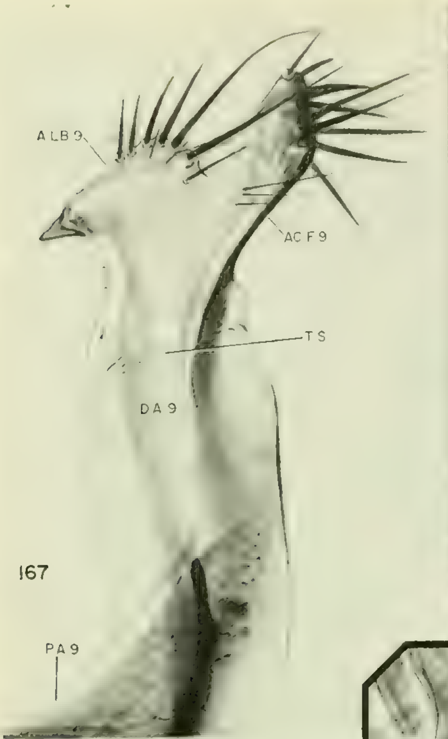

PAP
H
B.
D SP
BC
DIL P
9S.
OV
7S
DVG
GVG
VAG.
8S
8T
A.GREEN

163



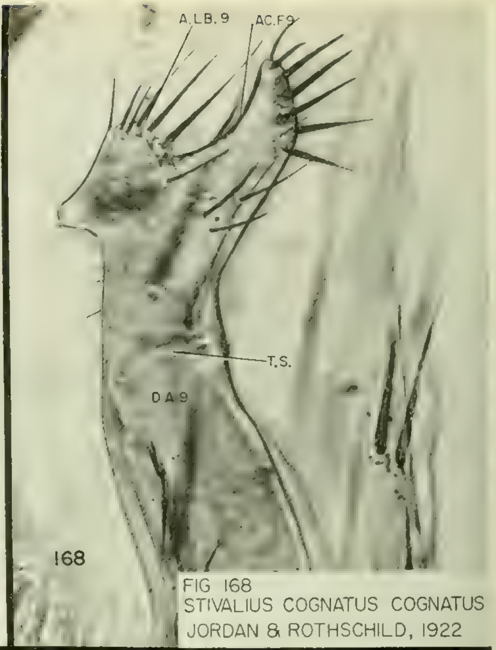
FIGS. 164-166
STIVALIUS COGNATUS BAMUS N.SSP.

E.B.
164
STV.
S.G.
D.FR.
V.A.L
F.
A.B.
U.L.7
C.P.
P.
F.S.
MB.
165
U.M.B.
A.B.
FRK.
U.L.7
L.M.B.
L.L.7
7SPC.
L.M.B.-2
8 SPC.
166
J NAVARRO


A LB 9
AC F 9
T S
DA 9
PA 9

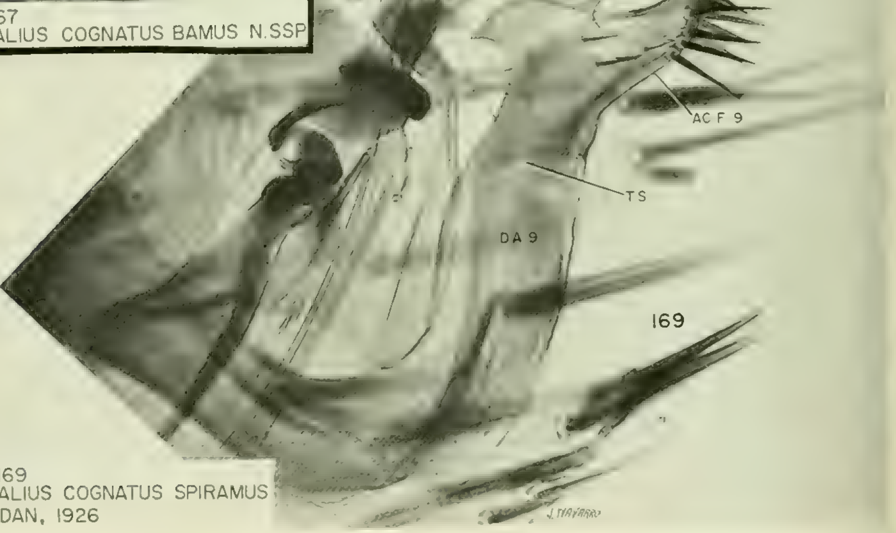
167

FIG. 167
STIVALIUS COGNATUS BAMUS N.SSP


A.LB. 9
AC.F9
T.S.
DA 9

168

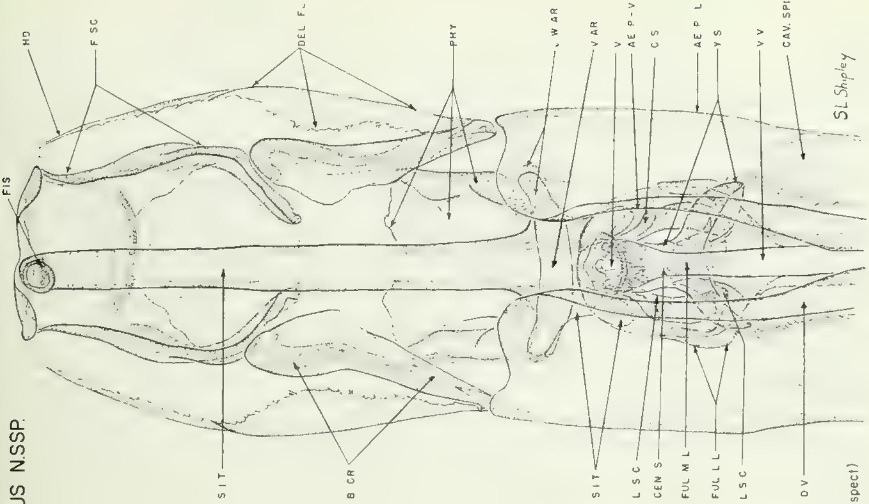
FIG 168
STIVALIUS COGNATUS COGNATUS
JORDAN & ROTHSCHILD, 1922


A.LB. 9
AC F 9
TS
DA 9
J. NAVARRO

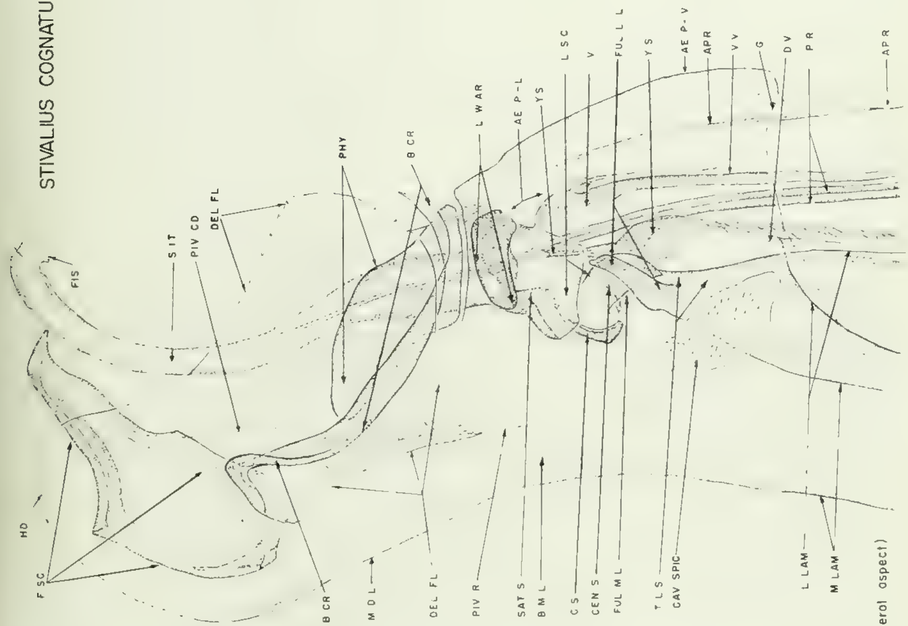
169

FIG 169
STIVALIUS COGNATUS SPIRAMUS
JORDAN, 1926

STIVALIUS COGNATUS BAMUS N.SSP.


HD
F SC
DEL FL
PHY
L WAR
V AR
V
AE P-V
C S
AE P L
Y S
V V
CAV. SPIC
FIS
S IT
B CR
S IT
L S C
CEN S
FUL M L
FUL L L
L S C
D V
SL Shipley

171 (ventral aspect)


FIS
HD
F SC
S IT
PIV CD
DEL FL
PHY
B CR
L WAR
AE P-L
YS
L S C
V
FUL L L
Y S
AE P-V
APR
V V
G
D V
P R
A P R
B CR
M D L
DEL FL
PIV R
SAT S
B M L
C S
CEN S
FUL M L
T L S
CAV SPIC
L LAM
M LAM

170 (lateral aspect)

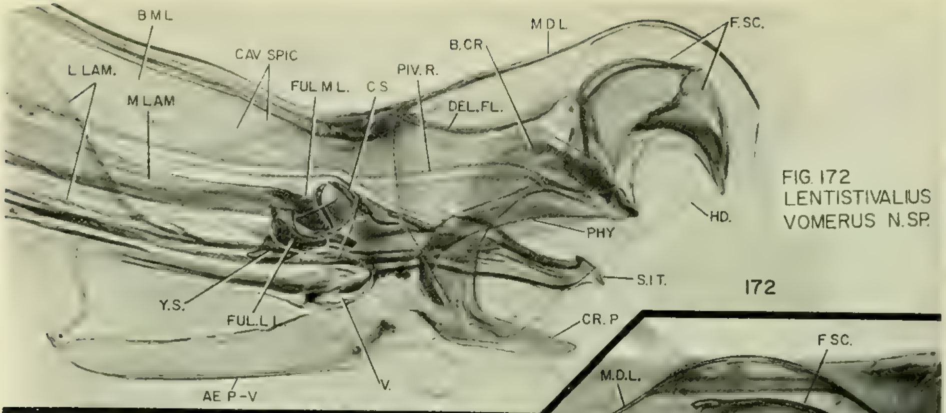

BML
MDL
F.SC.
CAV SPIC
B.CR
L LAM.
PIV.R.
FUL M L.
C S
M LAM
DEL.FL.
HD.
PHY
S.I.T.
Y.S.
FUL.L.L.
CR.P
V.
AE P-V
172

FIG. 172
LENTISTIVALIUS
VOMERUS N.SP.

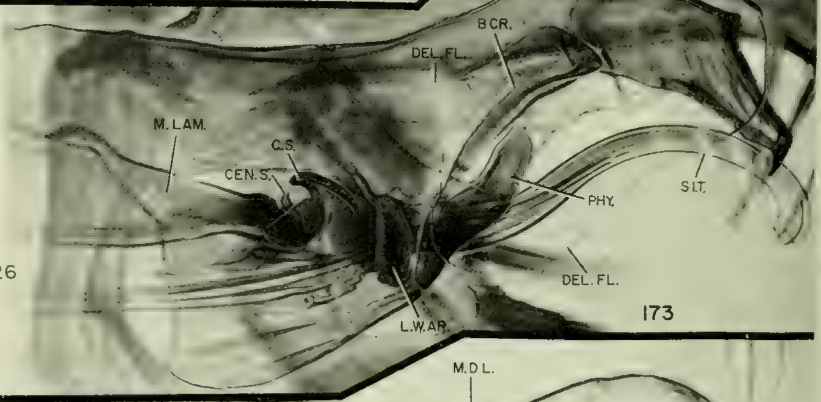

F SC.
M.D.L.
B CR.
DEL.FL.
M.LAM.
C.S.
CEN.S.
PHY.
S.I.T.
DEL.FL.
L.W.AR.
173

FIG. 173
STIVALIUS
COGNATUS
SPIRAMUS
JORDAN, 1926

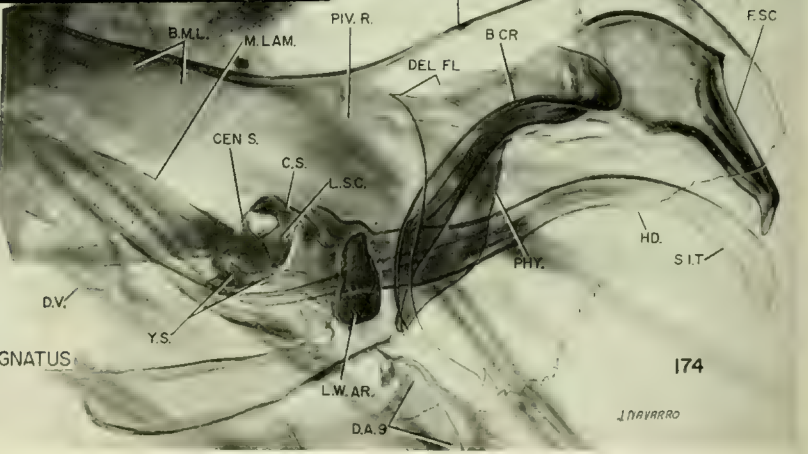
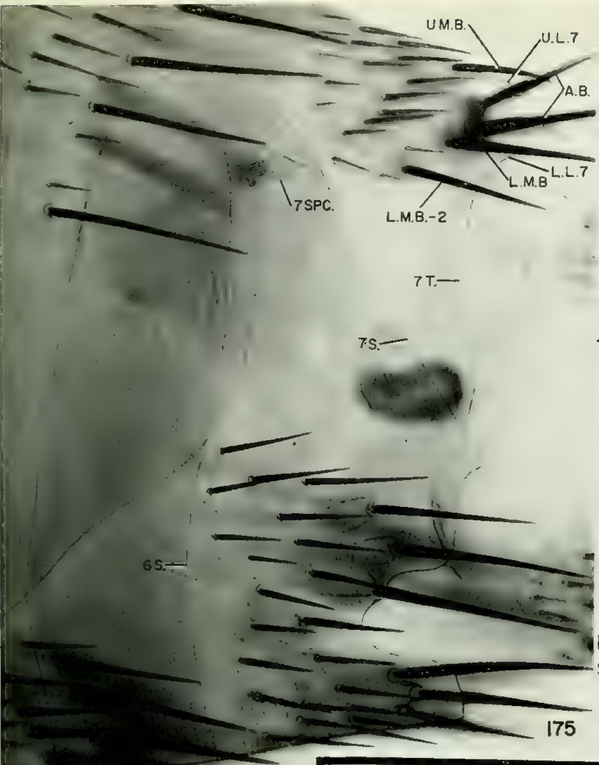

M.D L.
F.SC
PIV. R.
B.M.L.
M.LAM.
B CR
DEL FL
CEN S.
C.S.
L.S.C.
HD.
PHY.
S I.T.
D.V.
Y.S.
L.W.AR.
D.A.9
174
J NAVARRO

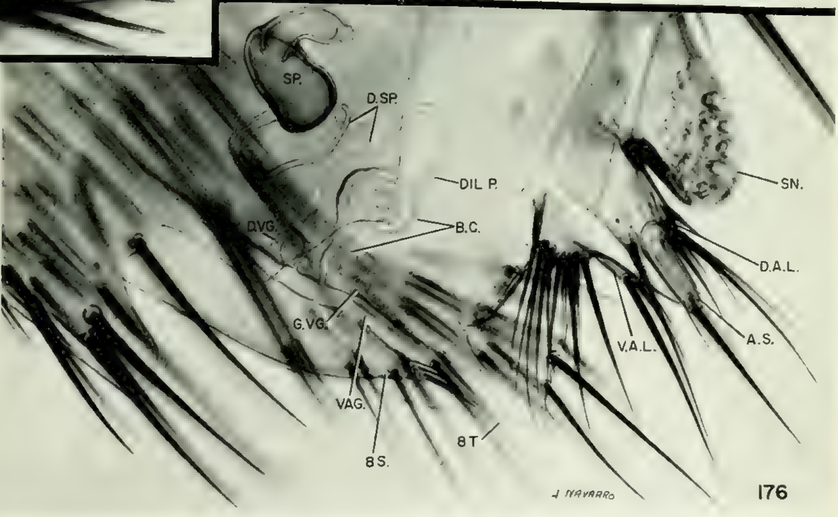
FIG. 174
STIVALIUS COGNATUS
BAMUS N.SSP.


U.M.B.
U.L.7
A.B.
L.L.7
L.M.B
L.M.B.-2
7SPC.
7T.
7S.
6S.

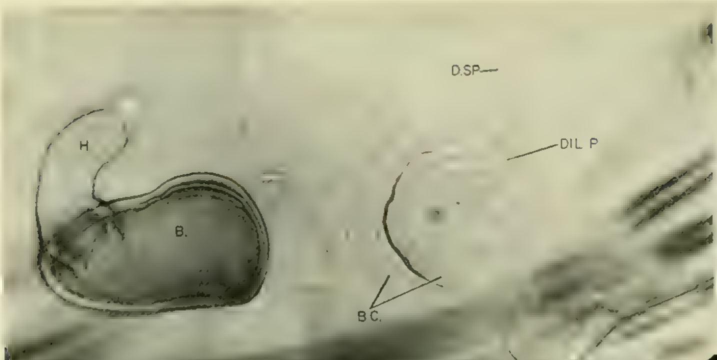
175

FIG. 175
← STIVALIUS COGNATUS SPIRAMUS
JORDAN, 1926

FIG. 176
STIVALIUS COGNATUS BAMUS N.SSP.
↓


SP.
D.SP.
DIL. P.
SN.
D.V.G.
B.C.
D.A.L.
G.V.G.
V.A.L.
A.S.
VAG.
8T
8S.
J NAVARRO

176


D.SP
DIL P
H
B.
B C.
177

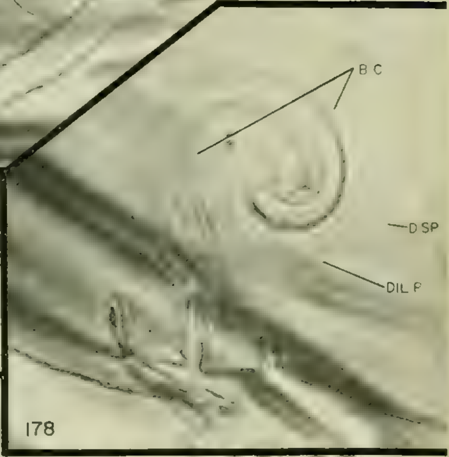

B C
D SP
DIL P
178

FIG. 177
STIVALIUS COGNATUS BAMUS N.SSP.

FIG. 178
STIVALIUS COGNATUS SPIRAMUS
JORDAN, 1926

FIG. 179
STIVALIUS COGNATUS COGNATUS
JORDAN & ROTHSCHILD, 1922

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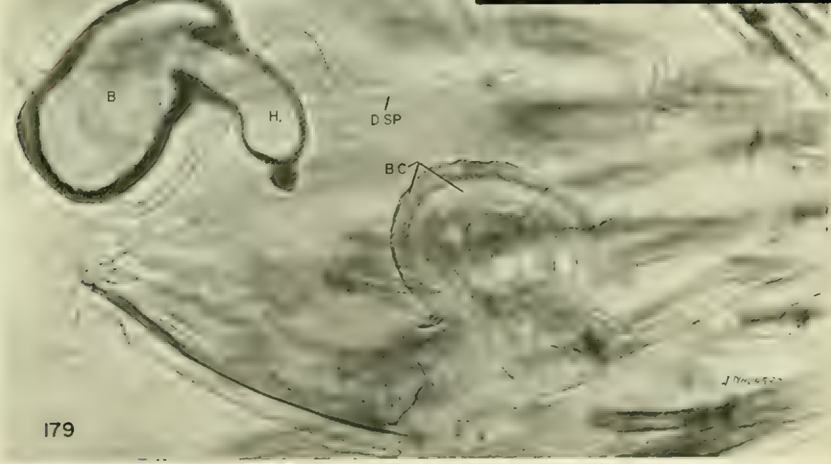
B
H.
D SP
B C
179

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II. CONVERGENT EVOLUTION

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University of Maryland

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ERRATUM

Page 354, third line from end of second paragraph:
for 'areas) or are mane-fleas. The archurieopsyllines include . . . '
read 'areas) or are murine-fleas. The archaeopsyllines include . . . '.

967

)LUTION AND TAXONOMY OF FLEAS (SIPHONAPTERA), BASED ON COLLECTIONS FROM GUNONG BENOM AND ELSEWHERE IN SOUTH-EAST ASIA.

II. CONVERGENT EVOLUTION

By ROBERT TRAUB

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ABSTRACT

In the Order Siphonaptera there are many examples of the moulding effect of the environment be it the fur or feathers of the host or its habitat —upon the physiognomy of the flea, resulting in a uniformity of appearance that may reflect convergent evolution, and not phylogeny or even homology.

Additional data are presented suggesting that the pattern and shape of the spines of the pronotal comb of fleas may be more frequently adaptive than had been generally supposed, as indicated by the fact that unrelated fleas often have the same type of comb (or vestiture in general), while, in contrast, a variety of patterns may be exhibited by a single genus of flea, depending upon the host. Thus, in the squirrel-fleas in general, the second or third spines of the comb (counting from the bottom) tend to be relatively broad, and often slightly overlapping near the base. This has been noted in 13 genera and 3 families of fleas, and in all instances these spines are proportionately broader and shorter than in the case of members of the same taxon which are "fur-fleas" of murids, cricetines, insectivores, etc. The trend is particularly well developed in fleas of diurnal tree-squirrels and has occurred on all four continents where these rodents occur. It is believed that modifications of this sort are directly associated with the diameter and shape of the hairs of the host, and it seems likely that the overlapping second and third spines of the comb of fleas of tree-squirrels would grasp the hairs in a scissors-like grip if the flea were pulled backwards by the host in attempts at dislodgement. Precise data on this point are lacking insofar as concerns fleas of squirrels.

The modifications of the pronotal comb are by no means always correlated with the vestiture of the host, as is indicated by the fact that, regardless of host, 17 genera of fleas, representing 3 families and 5 subfamilies, exhibit the same unusual type of ctenidium, in which the spines are exceptionally or notably short and broad and relatively few in number. These are all "nest-fleas" in that they are much more prevalent in the nest than on the host, etc. and show reduction in general chaetotaxy, modifications of the thorax and other specialized features. The type of comb in these fleas is accordingly believed to represent a general trend towards reduction which is a feature in the evolutionary development of the nest-habit, which is discussed in detail.

Fleas of volant and gliding hosts such as bats, birds and flying-squirrels have solved the dilemma of finding such a bird or mammal without a disastrous fall in the process and yet managing to remain affixed to the host despite its active flight or aerial gymnastics. One common way this has been accomplished is by becoming crawlers, rather than jumpers, and developing supernumerary spines in the pronotal comb, and/or additional combs, long bristles, etc. or by anchoring mouthparts. Such fleas often possess a thorax in which the pleural arch, under which is housed the elastic resilin which provides the power for leaping, has become completely or partially reduced. This thoracic modification is also seen in "nest-fleas" inhabiting tall trees, banks and caves, etc., where a fall would be hazardous, even if survived, because of the small chance of finding a suitable host. It likewise occurs in many nest-fleas of terrestrial or underground nests, and in other habitats, and reasons are advanced to indicate that the condition (in all cases) is adaptive. This modification of the thorax has been achieved by a variety of morphological changes, emphasizing that these are examples of convergent evolution.

The relative degree of the development of the eye in fleas is also associated with the habits of the flea, or its host or environment. In many instances, reduction of the eye accompanies that of the metathorax and loss of the pleural arch, but notable exceptions are pointed out. The behaviour of various kinds of fleas in finding and feeding on their hosts is discussed.

I. INTRODUCTION

FLEAS are highly modified morphologically for an ectoparasitic existence (Rothschild, 1917; Ioff, 1929; Traub, 1966; Traub & Evans, 1967), and the specializations exhibited include patterns of ctenidia (combs of spines) and chaetotaxy that somehow reflect the environment provided by the host (Traub & Barrera, 1966; Humphries, 1966, 1967; Traub, 1968, 1969), rather than merely the phylogeny or taxonomic position of the flea. The modifications in some instances are obviously adaptive and are concerned with the flea maintaining a grip on the host and escaping capture. Others are difficult or impossible to explain by referring to the vestiture of the infested mammal or bird, but can be correlated with the haunts or habits of the host. Some of the fleas discussed in the first article in this series (Traub, 1972a) illustrate such examples of Convergent Evolution, and these and other relevant taxa will be treated in the present paper and new points will be presented along such lines.

That the nature of the pronotal comb is adaptive is indicated by two generalizations: (1) The same pattern of comb is frequently exhibited by unrelated fleas parasitizing the same host, and (2) Within a genus there may be a variety of types of combs, depending upon the host. Therefore, by way of background, variations of the type of pronotal comb seen in a single taxon will be mentioned and associated with certain kinds of hosts. The characteristic features of the class of pronotal comb will be noted, and tabled data and illustrations will be presented for various genera of fleas, and for various kinds of fleas, such as squirrel-fleas, murid-fleas, nest-fleas, etc. In the section on discussion, it is pointed out that while in many instances the precise configuration of the comb can be explained by the nature of the hairs of the host, this does not apply to the type of comb seen in fleas which are characteristic inhabitants of underground nests, and which are modified accordingly, even though a variety of taxa, often unrelated, are represented. In order to demonstrate that this is so, and to offer an explanation, the phenomenon of nest-fleas is discussed in some detail and this leads to a consideration and review of two features commonly seen in nest-fleas, viz., the marked reduction of the eye and loss of the pleural arch. It is pointed out that in some nest-fleas, however, the eye is unusually large and this is shown to be adaptive, as is the loss of the pleural arch in bat-fleas, which are not nest-fleas. Thus, the morphological modifications are shown to be connected with the pattern of life of the flea, and often with the habits of the host.

It should be noted that no attempt is made in this article to review all of the various modifications in the pattern of pronotal combs seen in Siphonaptera. For example, the remarkable and well-known convergence exhibited by combed bird-fleas, in which the pronotal comb always bears a significantly greater number of spines than do allied forms infesting mammals, and which are otherwise specialized, will be treated in detail in a subsequent article. This phenomenon has now been noted in nine genera, representing three families (including a new genus and new records known to the writer). The type of comb deemed characteristic of fleas infesting nocturnal arboreal hosts has been mentioned previously (Traub, 1969), while Traub & Evans (1967) referred to some ctenidia of insectivore-fleas and desert-fleas, etc. and Traub & Barrera (1966) discussed ctenidia in shrew-fleas. Other points about ctenidia were treated by Traub in 1968, and some important considerations remain for future treatment. Instead, the present paper will primarily deal with the pronotal comb of fleas infesting arboreal squirrels and with that of nest-fleas in general, with passing reference to murid-fleas, etc., while, the resulting discussion leads to the points mentioned above.

II. BACKGROUND

The pronotal comb of *Medwayella* Traub, 1972 (fig. 6),[1] a genus which generally infests arboreal and semi-arboreal sciurids, resembles that seen in genera of fleas which are characteristic parasites of tree-squirrels (figs 1–14). However, before considering that subject further, it is instructive to review the features of the pronotal comb in some other fleas, particularly *Lentistivalius* Traub, 1972, in which the 5 known species are closely allied, as indicated in the article on *Medwayella*, but which vary considerably in the kind of host infested and their geographical location. In this group of fleas it has been possible to glance at the spines of the comb and correctly state whether the host is a bird, rodent or shrew. Although no bird-fleas had been known in the family Pygiopsyllidae prior to 1950, the author of *L. insolli* (Traub, 1950b) suggested that the species infested birds because the pronotal comb (vide fig. 18) consisted of 26–28 narrow, fairly straight, closely set spines and the comb did not extend far enough ventrad to cover the third vinculum, thereby paralleling the condition in bird-fleas of the families Ceratophyllidae and Leptopsyllidae. (This belief about the avian hosts of *L. insolli* turned out to be correct.) In each instance, the mammal-infesting fleas related to all of these bird-fleas bear combs of 18–24 spines (generally around 20), while the spines are broader, differently shaped, i.e. concave or pointed, or else, if there is a larger number of spines present, the comb extends further ventrad, over the vinculum (Traub, 1969). On the other hand, when Smit (1958) described the flea now called *L. alienus*, he pointed out that the appearance of the comb (vide fig. 16) led him to state that the host was a rodent, because the spines were "fairly straight," unlike *L. ferinus* (Rothschild, 1908) which is a shrew-flea, where "the spines are blunt, distinctly curved and longer than the pronotum," as shown in fig. 15. A comb of the latter type is characteristic of many shrew-fleas (Smit, 1958; Traub & Barrera, 1966; Traub & Evans, 1967), and is in marked contrast to the fairly straight, pointed spines of *L. aestivalis* (Jameson & Sakaguti, 1954) (fig. 19). The spines of the comb of *L. vomerus* Traub, 1972, which is primarily a tupaiid-flea,[2] are longer and narrower (fig. 17) than in *L. ferinus*.

---

[1] Unless otherwise indicated, the figures of combs herein are of male specimens.

[2] In modern schemes of classification, the tree-shrews (Tupaiidae) are either placed with the primates or as a sub-order of Insectivora (along with macroscelids), distinct from ordinary shrews and moles.

It seems surprising that a "simple" structure such as the pronotal comb should be so flexible or adaptive in evolution, and hence it is worth emphasizing that there are other genera of Siphonaptera where several kinds of pronotal combs are found within the one taxon, depending upon the host-affinities of the species concerned. For example, this is the case in *Ctenophthalmus* Kolenati, 1856, where the great majority of the approximately 100 species parasitize microtine and murid rodents, and have pronotal combs of the type shown in figs 22 and 26, viz., the spines are quite straight and broadly coming to a point apically. In contrast, in the *Ctenophthalmus* which are shrew-fleas (e.g., figs 21 and 25), the spines are generally concave and bluntly rounded apically, while mole-fleas have spines which are straight, very narrow and acutely pointed (fig. 24, and similar modifications in mole-fleas of other genera are cited by Traub & Evans, 1967). The combs of *Spalax*-infesting members of this genus (fig. 28) tend to be quite straight and fairly narrow, but not as stiletto-like as the talpid-fleas. All of the groups of *Ctenophthalmus* mentioned thus far possess combs in which the majority of the spines are definitely longer than the pronotum, but this is not the case for the few species that parasitize sciurids (*Citellus* ground-squirrels) (viz. *C. pollex* Wagner & Ioff, 1926, fig. 23). In the latter instance, the spines are proportionately shorter and broader than in the foregoing species, while the third spine from bottom (herein designated as spine number 3) is somewhat broader than the others. This last point is significant because, oddly enough, this spine is generally broad (especially at the base) in all fleas of diurnal arboreal squirrels, as will be shown. This spine is relatively broad even if those above the more dorsal ones are somewhat narrower, but usually number 2 or number 4 spine is nearly as stout as number 3.[3]

III. DATA AND OBSERVATIONS

A. THE PRONOTAL COMB

There are other instances of taxa in which the pronotal combs of the members vary in configuration according to the host, and the number of examples that can be cited indicated that this is true convergence and is based on an actual principle. Thus, in the Holarctic ceratophyllid genus *Monopsyllus* Kolenati, 1857 (iii.1),[4] which infests a variety of cricetid and sciurid hosts, it can be seen that the spines, particularly spine number 3, are broader (especially at the base) and shorter, and fewer in number in the species illustrated in figs 62, 64 and 66, which are true fleas of diurnal tree-squirrels, than in figs 55, 57, 59 and 61, which pertain to fleas of non-sciurids. The spines of the comb of the dormouse-flea (fig. 60) and of the flying-squirrel flea (fig. 58) are also longer and narrower than those of the fleas of diurnal squirrels, and exceed them in number.

---

[3] The hyperdevelopment of a single spine of the pronotal comb reaches a bizarre zenith in the pygiopsyllid genus *Traubia* Smit, 1953a. Smit described this genus on the basis of one species, and cited as a generic character the fact that the number 2 spine was much longer than its mates. Today there are 9 species of *Traubia* known to me, and all possess this odd feature, which seems to be unique in the Order. This development, however, is in a single taxon, unlike the case of the stout spines in the squirrel-fleas.

[4] The families and subfamilies are designated by Roman and Arabic numbers, e.g. iii.1, and a list of the names for these taxa are appended.

Other examples of this trend are provided in the genera *Orchopeas* Jordan, 1933 (iii.1), *Opisodasys* Jordan, 1933 (iii.1) and *Neopsylla* Wagner, 1903 (i.7), some of which parasitize arboreal sciurids while others infest other kinds of hosts. In *Orchopeas*, the spines of the squirrel-fleas (figs 29, 31, 33 and 35) are significantly broader and shorter than are those of *O. sexdentatus* (Baker, 1904) (figs 30 and 34) and *O. leucopus* (Baker, 1904), which are fleas of peromyscines. Similarly, in *Opisodasys keeni* (Baker, 1896) (fig. 43) and *O. nesiotus* Augustson, 1941 (fig. 45) which infest *Peromyscus*, the pronotal spines are noticeably longer and narrower, and the comb extends further down, than in the case of fleas of diurnal tree-squirrels (figs 44, 46 and 48). The comb of *O. pseudarctomys* (Baker, 1904) (fig. 47) is worthy of special note. Its spines are more numerous and narrower than in the case of the fleas from the diurnal squirrels, and as noted below (Section C.4), combs of this type are characteristic of fleas parasitizing nocturnal, arboreal species. In *Neopsylla*, in which the majority of the 34 species known to me infest murines or cricetines, the combs of fleas of chipmunks or ground-squirrels (figs 37, 39 and 41) bear spines that are proportionately definitely shorter and broader than in the murid-fleas (figs 38, 40 and 42).

The second principle, namely that the combs of sundry fleas of a particular kind of host tend to converge to a uniform configuration, is well shown in the fleas of arboreal or semi-arboreal squirrels. Thus, figs 1–14 illustrate the pronotal combs of 14 species of fleas of such squirrels, representing 13 genera and 3 families of fleas, and it can be seen that in all of these, the spines in general, and at least numbers 2–4 in particular, are broader and proportionately shorter than those of fleas infesting insectivores (figs 21, 24 and 25), murids (figs 49–54, 38, 40, etc.), and the peromyscine cricetids *Peromyscus* (vide figs 36 and 43), and *Neotoma* (fig. 32). For example, spine number 3 of the pronotal comb is 4·2 times as long as broad near the base in the case of *Aenigmopsylla grodekovi* Sychevsky, 1950 (fig. 9); 4·1 times in *Macrostylophora h. hastata* (Jordan & Rothschild, 1921) (fig. 14) and 3·1 for *Libyastus infestus* (Rothschild, 1908) (fig. 13), all of which are ceratophyllid squirrel-fleas, and 4·6 in *Medwayella robinsoni* (Rothschild, 1905), a pygiopsyllid from squirrels. In contrast, the ratio of the dimensions of this spine is 5·5 in *Lentistivalius ferinus* (Rothschild, 1908) (fig. 16), and 6·2 in *Ctenophthalmus* (*Alloctenus*) *cryptotis* Traub & Barrera, 1966 (fig. 20) both of which are shrew-fleas; 5·5 in *Neopsylla dispar* Jordan, 1932 (fig. 40) and 5·4 in *Stivalius cognatus bamus* Traub, 1972, both of which infest rats.

Attention is directed to the fact that in fleas of arboreal or semi-arboreal squirrels in general, and especially in those of diurnal species, pronotal spines numbers 2 and 3 are particularly broad near the base, and number 2 tends to overlap number 1 proximally, while the base of number 3 is usually very close to that of number 2 or overlaps it.

In this regard it is important to note that the greater breadth of the spines in proportion to length, which is here indicated as being characteristic of squirrel-fleas, is a relative feature, not an absolute one that can be expressed in an "average" ratio of length to width. Thus, while it is a general rule that the spines of the combs of squirrel-fleas are shorter and broader than those of fleas infesting non-sciurid hosts, it is also necessary to consider the norm for the taxon in question, for any modification of a pronotal comb must be incorporated upon an existing framework. It is

TABLE 1

RELATIVE PROPORTIONS OF CERTAIN PRONOTAL SPINES OF SQUIRREL-FLEAS AS COMPARED WITH THOSE OF FLEAS OF OTHER HOSTS

Sciurid Host	Flea	Ratio* Comb/Pro-notum	No. 3 Spine Length/Width	No. 3 Spine Length/Width	Ratio* Comb/Pro-notum	Flea	Non-Sciurid Host
Chipmunk	*Megabothris acerbus* (Jordan, 1925)	0·9	3·5	4·4	1·1	*Megabothris quirini* (Rothschild, 1905)	*Microtus*
Chipmunk	*Monopsyllus e. eumolpi* (Rothschild, 1905)	1	3·2	5·1	1·1	*Monopsyllus thambus* (Jordan, 1929) Fig. 57	*Peromyscus*
Tree-Squirrel	*Monopsyllus vison* (Baker, 1904) Fig. 64	0·9	3·7	4·8	1·2	*Monopsyllus exilis* (Jordan, 1937) Fig. 55	*Onychomys*
Palm-Squirrel	*Nosopsyllus ceylonensis* Smit, 1953	1·4	3·7	4·6	1·3	*Nosopsyllus l. londiniensis* (Rothschild, 1903) Fig. 49	Rats
Tree-Squirrel	*Opisodasys hollandi* Traub, 1947 Fig. 44	0·7	4·8	5·5	1·1	*Opisodasys keeni* (Baker, 1896) Fig. 43	*Peromyscus*
Tree-Squirrel	*Orchopeas howardi* (Baker, 1895) Fig. 2	1·2	3·7	5·1	1·3	*Orchopeas leucopus* (Baker, 1904) Fig. 36	*Peromyscus*
Tree-Squirrel	*Orchopeas n. nepos* (Rothschild, 1905) Fig. 29	1·0	3·6	5·3	1·4	*Orchopeas neotomae* Augustson, 1943 Fig. 32	*Neotoma*
Citellus (Ground-Squirrel)	*Ctenophthalmus pollex* Wagner & Ioff, 1926 Fig. 23	1·1	5	6	1·5	*Ctenophthalmus bisoctodentatus* Kolenati, 1863 Fig. 24	Talpids
Citellus (Ground-Squirrel)	*Neopsylla inopina* (Rothschild, 1915) Fig. 39	1·2	3·5	5·2	1·4	*Neopsylla luma* Traub, 1954 Fig. 38	*Rattus*
Tree- & Ground-Squirrels	*Medwayella robinsoni* (Rothschild, 1905) Fig. 6	0·8	5·4	6·2	1·2	*Stivalius klossi* (Jordan & Roths., 1922) Fig. 20	*Rattus*
Tree-Squirrel	*Pleochaetis soberoni* Barrera, 1958 Fig. 12	1·0	3·8	5·2	1·2	*Pleochaetis mathesoni* Traub, 1950	*Peromyscus*

* Ratio: Comb/Pronotum = length of horizontal subdorsal/length of dorsal margin of notum.

patently absurd to expect a combless flea parasitizing an African ground-squirrel to develop broad spines, especially if descended from combed ancestors, for according to Dollo's Law, structures lost in the course of evolution cannot be resurrected *per se*, as discussed by Jordan in 1947 and by Traub in 1968 and 1969. Similarly, in a taxon where the pronotal spines are in general fairly narrow, the response to parasitism of squirrels could not be validly expected to equal that in *Orchopeas*, where the spines tend to be fairly broad in all species, regardless of host. In *Nosopsyllus* Jordan, 1933 the spines are quite broad, as a rule, and hence in that genus an "average" index of length to breadth would exceed the standard for *Ctenophthalmus*. The best way to examine this hypothesis, therefore, is to compare various members of genera which parasitize both sciurid and non-sciurid hosts and see if there is a significant difference. Such a comparison is presented in Table 1.[5]

From these data it can be seen that in each case, the squirrel-infesting species have pronotal spines that are significantly broader in proportion than those of its allies on other hosts. Moreover, as shown by the comparison with the length of the pronotum, which is also presented in the table, the spines of the comb of squirrel-fleas are also definitely shorter. There definitely is an inverse correlation between the length of the spines and that of the pronotum, as per what has been designated as the Principle of Totality of Mass (Traub, 1969).

Of the fleas reported from tree-squirrels, the one with the proportionately narrowest spines is the Central American ceratophyllid *Kohlsia graphis* (Rothschild, 1909). Here the number 3 spine is 4·3 times as long as broad near the base, and the dorsal spines are about 1·2 times as long as the dorsal margin of the pronotum. However, the comparable figures for the related *K. gammonsi* Traub, 1950 are 4·8 and 1·4 respectively, so there is a significantly greater relative breadth in *K. graphis*. However, it should be noted that it is not certain that the latter is truly a squirrel-flea. Apparently there are only about 24 specimens known (in all collections extant), and although virtually all of these are from squirrels (Nicaragua, Costa Rica, Panama, etc.), Tipton & Méndez (1967) could only find 16 on a total of 60 *Sciurus granatensis chiriquensis* in Panama, all of which had been carefully examined for fleas. It may be that the true host has not yet been discovered, but my belief has been that *K. graphis* has only relatively recently transferred to squirrels. Tipton & Méndez (1967) have independently come to a similar conclusion regarding *Kohlsia* Traub, 1950 in general in Panama, and state that it "may be that some of the true hosts no longer occur in this area and certain of the present hosts have been 'adopted'."

It should also be borne in mind that these differences are consistent within the taxon, i.e. the samples are representative of the comb of squirrel-fleas whether only a few members infest arboreal or semi-arboreal squirrels, e.g. 1 of 24 for *Kohlsia*, 1 or 2 of 23 for *Pleochaetis* Jordan, 1933, 1 of 12 *Paraceras* Wagner, 1916, 6 of 46 *Nosopsyllus*; or whether the majority of the species do, viz. all 28 species of *Macrostylophora* Ewing, 1929, 12 or 13 of 13 species of *Medwayella*, 8 of 11 *Orchopeas* and 16 of 22 *Monopsyllus*. An idea of the comparative differences in the proportions that are involved may be gained by reviewing the illustrations of sundry *Orchopeas* (figs 29–36), *Opisodasys* (figs 43–48), *Monopsyllus* (figs 55–66) and *Neopsylla* (figs 37–42).

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[5] Inasmuch as no *Medwayella* are known to consistently infest non-sciurids, the representative species in the table is compared with a member of a related genus.

A further illustration of the principle that the fleas of a particular kind of host tend to disport the same type of pronotal comb is provided by *Neopsylla*. It is to be noted that in the murid-species (figs 38, 40 and 42), the pronotal spines are relatively long, narrow and straight. This is characteristic of murid-fleas in general (Traub, 1968) and examples are shown in figs 49–54, depicting combs of murid-fleas from 3 families, infesting such hosts as *Mus*, *Apodemus* and subgenera of *Rattus*. Additional examples may be seen in figs 19 and 20.

B. The Pleural Arch

For an Order that is often thought of as "homogeneous," there is a surprising amount of variation on the structure of the Siphonapteran thorax, and to a considerable extent the differences represent adaptive changes and not phylogeny, as will be noted in the section on Discussion. One of the major elements involved is the so-called pleural arch, which is present and well developed in some species and reduced or absent in others, and the two extremes may at times be seen within one genus, viz, well developed in *Opisodasys hollandi* Traub, 1947 (iii.1) (fig. 87, PL.A.) and *Ceratophyllis styx* Rothschild, 1900 (iii.1) (fig. 91, PL.A.) but absent in *O. vesperalis*°[6] (Jordan, 1929) (fig. 88) and *C. arcuegens*° Holland, 1952 (fig. 90). It is fairly well developed in *Xenopsylla vexabilis* Jordan, 1925 (ix.1) (fig. 93, PL.A.) but so reduced as to be virtually absent in *X. papuensis*° (Jordan, 1933) (fig. 92, PL.A.(?)).

In each of the above instances where the pleural arch is well developed, the metathoracic region may be described as follows: There is a stout pleural rod (PL.R.) appearing as the margin between the metepisternum (MTS.) and metepimere (MTM.), arising from the dorsal portion of the base of the metacoxa and terminating at or about the ventrocaudal angle of the subquadrate lateral metanotal area (L.M.). The latter sclerite is quite well developed, e.g. longer than high, and as long as the third vinculum (VC.3) which links into it and at least several times as tall (high) as VC.3. Above the expanded dorsal apex of the pleural rod, which is at level of VC.3, or slightly lower, there is a conspicuous gap surmounted by the semi-ovate pleural arch (PL.A.). In *O. hollandi* the arch is at level of the middle of L.M. Above the pleural arch, the dorsal and caudal margins of L.M. merge and continue dorsad as the caudal margin of the metanotum (MTN.) and the base of the metanotal flange (MT.F.). The metepimere (MTM.) flanks the pleural rod and continues dorsad laterad to L.M. and then turns dorsocaudad and runs to the anterodorsal region of the first abdominal tergum (1 T.). The short thickening known as the squamulum (SQ.) serves as a good landmark for the anterodorsal region of the metepisternum.

In the two illustrated ceratophyllids which lack the pleural arch (*O. vesperalis*°, fig. 88 and *C. arcuegens*°, fig. 90), the pleural rod (PL.R.) terminates at the ventrocaudal angle of the lateral metanotal area (L.M.). In each case L.M. is narrower than in the species possessing PL.A., and in *O. vesperalis*°, L.M. bears heavily tanned internal margins and is quite ovate, while the pleural rod (PL.R.) is quite convex. In the pulicid, *X. papuensis*° (fig. 92), the pleural arch at first glance seems to be missing completely, but actually is a very narrow structure (PL.A.(?)) virtually hugging the apex of the pleural rod (PL.R.) near the ventrocaudal corner of the lateral metanotal area (L.M.); the cap is almost contiguous to the rod on the sides as well as on top. L.M. is fairly large and quadrate, but smaller than in *X. vexabilis* (fig. 93). The metepisternum (MTS.) extends higher and is longer than in other members of the genus.

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[6] ° denotes species in which the pleural arch is absent, or essentially so, and these are indicated thusly henceforth.

As can be seen in fig. 89, in the bat-flea *Nycteridopsylla eusarca*° (Dampf, 1908) (v.1), there is no sign of the pleural arch, and the lateral metanotal area (L.M.) is very narrow and longer than high. The pleural rod (PL.R.) is flat, and serves as the margin between the metepisternum (MTS.) and the metepimere (MTM.), which is not the case in some other ischnopsyllids, e.g. *Myodopsylla* Jordan & Rothschild, 1911, in which the caudal border of MTS. overlaps MTM. The two hystrichopsyllids shown in figs 85 and 86 likewise lack the pleural arch, but they present a thorax which is very different from the types described above (and differ from one another) but these are treated later, in the Discussion.

IV. DISCUSSION

A. The Function of the Pronotal Comb

1. General Comments. The modifications of the pattern of the pronotal comb consistently exhibited by shrew-fleas, bird-fleas, etc. should be adaptive, i.e. of some significant value to the insect, and the most obvious function for the specialized comb would be to serve as a device to prevent backward motion amongst the hairs or feathers of the particular host, for, as N. C. Rothschild pointed out in 1917, even non-combed fleas are unable to move backwards, thanks to the firm caudad-directed bristles of the body. Thus, the mere presence of a comb would facilitate ready *forward* passage through the hairs, but the inclination of the spines and the gaps between them would have to jibe with the structure and density of the hairs of the host before they could effectively prevent backward motion induced by teeth, beak or claws of the host intent on destroying or removing the flea. The various references cited in the Introduction include data and discussions on these points, and Humphries' articles (1966, 1967) include specific measurements showing how, in designated instances, the combs of a variety of fleas are so framed that they effectively entrap the hairs of the host in backward locomotion. Ioff, as early as 1929 tried to account for the unusual, short, pale, bluntly pointed or rounded genal spines in *Ctenophthalmus* (*Neoctenophthalmus*) *dilatatus* Wagner, 1928 in terms of the "extremely thick soft silky fur of the hosts of this flea" (the burrowing mole-rat, *Myospalax*).[7]

2. Special kinds of Combs on Fur-Fleas. In speaking of fleas which move about fairly freely in the pelage of the host, viz., the species which Ioff (1929) called

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[7] Ioff (1929) also speculated that the type of genal comb in *C. dilatatus* represented an acceleration or development of the trend in this group of fleas towards variation in number and reduction in size of the spines of the genal comb. He thought this evolutionary trend might be due to the frequency of overt damage to ctenidial spines seen in these fleas. (Such broken spines are often seen in fleas of other fossorial hosts as well—R.T.)

"fur-fleas," Traub (1968) pointed out that fleas with stiletto-like pronotal spines are characteristic parasites of peramelid marsupials (bandicoots) while their close relatives on rats have bluntly pointed spines and that these ctenidia correlate well with the nature of the fur of the host. Holland (1969) also independently observed the convergence of the pointed spines seen in the pronotal comb of most bandicoot-fleas. Recent collections in New Guinea provide new data reinforcing this hypothesis. Thus, on the basis of the six species then known, Holland (1969), when describing *Papuapsylla*, understandably concluded that the pronotal spines were characteristically bluntly pointed or rounded at the apex. These species infest sundry rats, and the same is true for the minimum of eight new species of *Papuapsylla* known to me which possess a similar type of comb of broad, subrounded, slightly upcurved spines. However, two undescribed *Papuapsylla* from bandicoots have combs with spines that are straight and relatively acutely pointed, again indicating the moulding-influence of the vestiture of the host upon the flea.

Humphries (1966) well demonstrated how the pronotal spines of certain fleas (which were not squirrel-parasites) "appeared to be structured in relation to the host's hair," and there can be little doubt that the processes of natural selection have tailored the pronotal combs to conform with the host-pelage in many instances. It seems likely that this may also be the case in the fur-fleas of diurnal arboreal and semi-arboreal squirrels, for, as shown above, all the combed species exhibit essentially the same type of ctenidium, even though a variety of taxa of fleas and many genera of sciurids and four continents are involved. Not only do these combs bear relatively broad spines subventrally, but, the bases in particular are broad, and the gaps between spines number 1 and number 2 and spines number 2 and number 3 are not only acute proximally, but often overlap at the base. As a result, any hair slipping between the teeth would be grasped in a scissors-like vise if the flea were pulled backwards. Moreover, this modification seems to be at the precise height to best grasp the axil of the hairs in their normal position. However, this hypothesis needs testing by experimentation and careful measurements, for we lack such data, and further, the theory implies that the sundry squirrels have a basically similar type of vestiture, and we do not know if this is so. Nevertheless, the similarity of the hairs should not be expected to be precise, for the combs of squirrel-fleas are not fully uniform, viz, the spines in the fleas of semi-arboreal species like *Dremomys*, *Rhinosciurus*, *Lariscus* etc. are often somewhat narrower than those of fleas of truly arboreal squirrels. This can be seen in *Macrostylophora borneensis* (Jordan, 1926) (fig. 96), a flea of *Dremomys*, as compared to *M. hastata* (Jordan & Rothschild, 1921), a flea of tree-dwelling *Callosciurus*. This in turn suggests that the hairs of *Dremomys* are coarser than *C. erythraeus*. Simple comparative measurements alone will not suffice, however, for heed must be paid to the precise parts of the body of the squirrels where particular species of fleas are most apt to be found, because the sizes of the hairs vary, and so do the habits of different fleas (Traub & Evans, 1967). As those authors indicated, apparently there is limited mobility in the comb itself, so that it can be either somewhat appressed to the body or slightly removed from it, and this is another factor to consider. Certainly, however, the present writer can advance no other hypothesis but the matching of hairs and spines to account for the convergence in the pronotal combs of the fleas of diurnal, arboreal squirrels.

Holland (1964) reported that "*Archaeopsylla* spp. (Pulicidae) and *Bradiopsylla echidnae* (Denny, 1843) (Pygiopsyllidae) share a structural modification of the pronotal comb not otherwise known in either family," referring to the fact that the ctenidium consists of only a very few spines (dorsal in position) and that these are fairly well separated, very short and are broad at the base and apically pointed. Holland then went on to say that "it may be significant that the former infest hedgehogs (*Erinaceus*) which are spiny insectivores while the latter lives on echidnas (*Tachyglossus*) which are spiny monotremes". It seems to me that this noteworthy observation really does pertain to an example of true convergence in that the nature of the comb can be explained by considering the spinose vestiture of the host. That is, the broad gap between the pronotal spines would appear to correspond with the diameter of the spines of the host, and the short pronotal spines could successfully span the mammalian spines, fitting snugly and securely against them. In contrast, a comb of long spines could not do so unless the spines were extremely divergent apically far more so than is known in any flea, and, in fact, the apices of the spines would tend to overlap and cross one another. Moreover, the divergence between the short spines of these fleas of spiny animals presumably also accounts for the short height and dorsal position of the comb. A long comb is incompatible with subdorsal spines that are markedly divergent, for these spines would have to overlap and hence not function properly. That there is an intimate association between a short pronotal comb of small, widely spaced spines, and infestation of spiny animals is further suggested by the fact that the monotypic pulicid genus *Centetipsylla* Jordan, 1925, a parasite of Madagascar "hedgehogs" (tenrecs), has a comb of this type, while related genera, infesting non-spiny hosts, do not.

However, instances have also been cited where the relationship between comb of the flea and vestiture of the host cannot be so simple (Traub & Evans, 1967). An example of this is the "flared comb" of some shrew-fleas and macroscelid-fleas which arches back over the mesonotum, as described by these authors. Here the gap between some of the spines is inclined at nearly right angles to the longitudinal axis of the body, and hence it would be difficult for such a comb to grasp and retain hairs if the flea were in the usual position most fleas assume when feeding. However, if these particular fleas act like those noted in New Guinea which have marginal rows of spiniform bristles on the head (and/or flattened pronotal margins), and incline the body head-downwards and thus hook the hairs of the host (Traub, 1968, 1969), the flared comb may then be an effective mechanism against dislodgement. This hypothesis can be verified only by direct observation, however.

Another example of a type of comb which presumably is not directly associated with host-pelage is that characteristic of fleas found in the fur of mammals in desert areas, in which the teeth of the comb are long and narrow, are close-set at the base and point somewhat dorsad or laterad so that the apices are as remote as possible from the mesonotum (Traub & Evans, 1967). The *Orchopeas* of desert-*Neotoma* have combs of this pattern, viz, a subspecies of *O. sexdentatus* (fig. 34) and *O. neotomae*

Augustson, 1943 (fig. 32), in contrast to *O. sexdentatus agilis* (Rothschild, 1905) (fig. 30), from a mesic habitat.

3. THE PRONOTAL COMB OF FLEAS OF NON-ARBOREAL NESTS. The type of pronotal comb which is most difficult to associate with host-pelage is that exhibited by certain mammal-fleas which presumably characteristically infest the nests of their hosts (usually underground or on the surface) and which are seldom found on the mammals themselves, apparently feeding while the hosts are in the nests (Traub & Evans, 1967). Examples of the combs of fleas believed to be of this type are shown in figs 67–84, 86 and 98, and it will be noted that in these the spines are much broader and generally much shorter than those indicated for squirrel-fleas (and hence far more so than in shrew- and murid-fleas, etc.). In such combs there are only 6 or 7 spines per side, instead of the usual 8–10 or more, and the spines are only 3·5–4·5 times as long as broad, instead of 5–7 times or more. Some of the number 2 spines are so stout that they are scarcely thrice as long as broad. (Amongst fleas in general there is a good correlation between a low number of spines in the comb and unusually broad girth, as compared to large numbers of spines and narrow breadths, provided the comb is of full size, i.e. extends down to near the vinculum.)

It is remarkable how large a variety of fleas, from a large assortment of hosts and from widely separated parts of the world, present essentially this type of pronotal comb. Included in the illustrations are representatives from 17 genera from 3 different families of fleas and a total of 5 subfamilies. Geographically, North America, Central America and Asia are listed, while 12 genera of hosts are cited, and these refer to 2 orders; 2 families of 1 of the orders; 3 subfamilies of cricetids and 2 tribes of cricetines.

The question immediately arises as to why fleas of such diverse backgrounds should uniformly present a single morphological feature. It seems extremely unlikely that such a variety of hosts should converge to the same type of pelage and that hence the pattern of pronotal combs represents parallel development of spines adapted to fit the hairs of the host. Thus, if the type of pronotal comb were determined purely by the type of fur of the host, then there should be no difference between the pattern of ctenidium exhibited by a flea which feeds while in the fur of an active host and that of one feeding on that host in the nest. However, frequently the nest-flea has a markedly different type of pronotal comb than the flea living in the fur of precisely the same individual mammal, e.g. the nest-flea *Conorhinopsylla nidicola*° Jellison, 1945 (i.2) (fig. 86) versus the fur-flea *Orchopeas sexdentatus* (iii.1) (figs 30, 34) on *Neotoma*; *Phalacropsylla paradisea* Rothschild, 1915 (i.7) (fig. 78), versus *O. neotomae* Augustson, 1943) (iii.1) (fig. 32), also on *Neotoma*; or nest-fleas like *Catallagia charlottensis* (Baker, 1898) (i.7) (fig. 67) and *Delotelis telegoni* (Rothschild, 1905) (i.7) (fig. 74) in contrast to fur-fleas like *Monopsyllus wagneri* (Baker, 1904) (iii.1) (fig. 59) and *Opisodasys keeni* (iii.1) (fig. 43), which infest *Peromyscus*. Most of these genera of nest-fleas do not include fleas which also infest the fur of the hosts, but *Pleochaetis* is an instructive exception. *P. paramundus* Traub, 1950 (fig. 62) is the only representative which is believed to be a nest-flea and it has relatively short and broad pronotal spines. Amongst the other 22 species, the one with the broadest spines in the comb is the squirrel-flea, *P. soberoni* Barrera, 1958 (fig. 12) and, of course, its spines do not compare in breadth with those of the former species.

In order to explain the phenomenon of convergence of the pronotal comb to this type, it is necessary to digress and first discuss nest-fleas in general, as well as such topics as the pleural arch of the metathorax and the varying degrees of the development of the eye seen in various fleas, since morphological modification of these structures are marked in nest-fleas.

B. Nest-Fleas in General

1. Introduction. Various students of Siphonaptera have noted that certain groups of fleas are relatively seldom found on the bodies of their hosts but are nevertheless common within the nests of the mammal or bird concerned, and that these fleas are morphologically modified in various ways that reflect their pattern of life, viz., the tendency to remain in nest-litter or to crawl into cracks and crevices in the nest and to feed on their hosts while the latter are in their nests, perhaps while they are sleeping. Presumably they are found on the host only if the mammal or bird leaves the nest prematurely, as when frightened or during the breeding season, when the hosts rarely linger in the burrows, and thus the flea is interrupted in its feeding. As indicated below, the true nest-fleas differ substantially in appearance from "fur-fleas" which spend most of their time on the pelage of the host, even when active out of the nest, and are modified accordingly. However, before proceeding, it is necessary to point out that the term "nest-flea" has been used in several different senses. Ioff (1929) used it to refer to all species which were more common in the nest than on the host, even though they may have often been collected on the host, and even though they were adapted for living in the fur. Hubbard (1947) also noted that it was far easier to collect certain fleas in the nest than on the mammal. In 1941, Ioff pointed out that "fur-fleas" need frequent blood meals and apparently cannot survive if off the host for long periods, whereas the "nest-fleas" were only occasionally found on the hosts and could remain away from the mammals long enough to be able to hibernate in the nest in its absence. Ioff thus made distinctions that were physiological and ecological and of undoubted importance in the epidemiology of plague. Nevertheless, no further definition was given, and, indeed, probably would have been impossible because of the variations in degree that occur in the two groups of fleas, and because the habits of the fleas may vary with the season, etc. As will be shown, some bird-fleas feed avidly while the young are in the nest and then undergo prolonged fasting. Sazonova (1962) cited other examples of species "that feed more frequently than nest-fleas but are also able to survive for a long time in empty nests," and alludes to "such typical nest species as *Neopsylla setosa* [that] spend therefore a longer time on the host than usual" when the female fleas are maturing their eggs. For these reasons Zhovtyi (1960) validly advised against placing fleas in such ecological groups until such time as more information had been obtained about their habits, bionomics, etc. Zhovtyi later (1963) developed this theme further, and objected anew to classifying fleas into "nest" and "fur" categories, pointing out that in his view the fleas in question (*Citellophilus tesquorum* (Wagner, 1898), *Neopsylla setosa* (Wagner, 1898), *Ctenophthalmus pollex* and several species of

Xenopsylla) were all "more adapted to the nest than to the fur of their hosts and also spend more time in the nests than on the hosts themselves". An additional complicating factor was that the same species were found to be more prevalent in the nest than on the host at certain times or seasons, whereas at other times the reverse was true.

It should be borne in mind that Zhovtyi and the other Soviet authors were discussing differences in behaviour that are physiological in basis, depending upon the life cycles of the fleas (which in turn may prove to be attuned to the hormonal or physiological state of the host itself, as at times of hibernation or breeding) or, as Zhovtyi (1963) indicated, upon ecological conditions such as temperature or atmospheric humidity.

In the present paper, however, we are discussing other types (and other taxa) of fleas, e.g. those which are morphologically highly specialized for feeding upon their hosts when they are in repose in the nest, and which rarely accompany the mammal or bird out of the nest. These specially adapted fleas are herein referred to as nest-fleas because the term is convenient, has been used in the past in this sense, and because, for our purposes, it can be defined in terms of structural modifications. In this case too, it will be shown that there are varying degrees of specialization, but the concept of nest-fleas, is an important and useful one. The species called nest-fleas in the present paper are characterized by possessing several or many of the following features: (1) An eye which is rudimentary, vestigial or absent. (2) Reduction in chaetotaxy, including the numbers of rows of bristles and the numbers of bristles on various parts of the body, and in diameter of the bristles. Even the antepygidial bristles may be exceedingly few in number and/or be very thin, and even at times be present in females and absent in males, i.e. most Rhadinopsyllini. (3) Reduction in numbers of spines in combs, or the numbers of the ctenidia, or the height and length of the comb; or else the elimination of combs altogether. (4) A similar, but even more pronounced reduction in or elimination of the apical spinelets, viz., the so-called "minor combs." (5) Reduction of the thorax, including shortening of sclerites such as the lateral metanotal area; consolidation of parts; diminution in size of the pleural arch, or its loss altogether; or reduction in the degree of sclerotization of the metanotal flange, or in its size; and loss of its apical spinelets. (6) Legs relatively long and slender. (7) Lessening of the ability to jump, or concomitant increase in the facility of crawling and entering tight cracks. (8) Hyperdevelopment of certain structures, e.g. lengthening of stylets and labial palpi (at times with an increase in the number of joints), development of broadened sections of antennal segments which enclose other segments; or of lobes on the coxae, or of straight or angled anterior margins on some thoracic sterna; elongation of legs at times accompanied by development of a fringe of long bristles on the male hind tarsus. (9) Loss in degree of sclerotization of caudal margins of abdominal segments. This may be accompanied by hyper-sclerotization of the antero-dorsal portions. (10) Diminution in size. At least some of these points were mentioned by Holland, 1949, 1952, 1965; Hopkins & Rothschild, 1962; Lewis, 1969; M. Rothschild & Clay, 1952; Traub, 1950a, 1950b, 1952, 1953a, 1953b; Traub & Tipton, 1951; Traub & Barrera, 1966; Traub & Evans, 1967; and M. Rothschild, 1969. It is also apparent from the comments by N. C. Rothschild (1917) and Jordan (1937) on Convergent Evolution, as well as from their descriptive notes on *Phalacropsylla* Rothschild, 1915, *Anomiopsyllus*° Baker, 1904 and *Callistopsyllus*° Jordan & Rothschild, 1915 (vide N. C. Rothschild, 1915; Jordan & Rothschild, 1915) that these scientists were fully cognizant of such modifications and the correlation with nest-inhabitation, although they usually did not refer to the association by name.

The known acme of specialization as nest-fleas are in forms like *Anomiopsyllus*° and *Wenzella*° Traub, 1953, which lack combs, eyes, and the pleural arch entirely, and which have long slender legs and mouthparts. Even the apical spinelets, possessed by most fleas and believed to represent vestigial combs (Traub & Evans, 1967), are missing. In the former, the species are often virtually nude, or the few bristles present are short and thin. In *Wenzella*°, the bristles are very thin, while the intercalary bristles of the abdominal rows are virtually only vestiges. In *Jordanopsylla* Traub & Tipton, 1951, this process, which has been termed "evolution by loss" or "specialization by simplification" by Hopkins & Rothschild (1962) has proceeded to the point of reduction of the eye and pleural arch, but not to their complete elimination, although the combs are absent, the mouthparts elongate, legs lengthened, etc., etc. In *Megarthroglossus*° Jordan & Rothschild, 1915 the modifications include extremely long mouthparts, coupled with reduction in the eye and vestiture, loss of pleural arch, etc. and while there is a pronotal comb, it consists of only 7–8 short, broad spines per side. Other genera possess these attributes to varying degrees, and on these grounds, as well as the fact that the species involved have rarely been collected on reported hosts, the following are cited as examples of nest-fleas. (In many instances the nests of the hosts have been insufficiently studied to permit one to state that these fleas are actually more numerous in the nest than on the birds or mammals themselves.)

2. HYSTRICHOPSYLLID NEST-FLEAS. Amongst subfamilies of Hystrichopsyllidae, 7 of the 8 Anomiopsyllinae genera are deemed nest-fleas, viz.: *Anomiopsyllus*°, *Conorhinopsylla*° Stewart, 1930, *Callistopsyllus*°, *Eopsylla*° Argyropulo, 1946, *Jordanopsylla*, *Megarthroglossus*°, and *Wagnerina* Ioff & Argyropulo, 1934. The exception, *Stenistomera*° Rothschild, 1915, is discussed later as a special case. (From the ° mark, it can be seen that 6 of these genera lack the pleural arch.) Of the 7 known Rhadinopsyllinae, all of which have no pleural arch, *Rhadinopsylla*° Jordan & Rothschild, 1912, *Stenischia*° Jordan, 1932, and *Wenzella*° are regarded as nest-fleas. *Trichopsylloides*° Ewing, 1938, is probably a nest-flea, and is discussed further in Section IV.C.5. Of the 11 Neopsyllinae, at least 8 fall in the category of nest-fleas, namely, *Catallagia* Rothschild, 1915, *Delotelis* Jordan, 1937, *Epitedia* Jordan, 1938, *Genoneopsylla* Wu, Wu & Liu, 1966,[8] *Phalacropsylla*, *Paraneopsylla* Tiflov, 1937, *Strepsylla* Traub, 1950 and *Tamiophila* Jordan, 1938. (The exceptions are *Meringis* Jordan, 1937, *Neopsylla*, *Rothschildiana* Smit, 1952.) One of the 6 genera of

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[8] NEW SYNONYMY. *Evansipsylla* Traub, 1968 is a synonym of *Genoneopsylla* Wu, Wu & Liu, 1966, the description of which escaped my notice when the Chinese ceased filling subscriptions to their journals. The type-species proposed, *thysanota* Traub, 1968 is presumably different from the type of *Genoneopsylla*, namely *longisetosa* Wu, Wu & Liu, 1966, but one cannot be certain because of the lack of details in the sketches that illustrate *longisetosa*.

Ctenophthalminae seem to be a nest-flea, viz. the South American *Agastopsylla*° Jordan & Rothschild, 1923, as indicated by the marked reduction of the thorax, and in chaetotaxy, etc. It has been pointed out that the short pale spines in the genal comb, and their frequent variation in number (even on the two sides of the same specimen), all are suggestive of "an evolutionary tendency in the genus towards complete reduction of the comb" (Traub, 1952), while morphological similarities with anomiopsyllines were therein deemed examples of convergent evolution in unrelated nest-fleas.

It is possible that one of the 5 Doratopsyllinae may prove to be a nest-flea, viz. *Idilla*° Smit, 1957, an Australian marsupial-flea, in which there is rather great reduction in chaetotaxy and loss of the pleural arch. However, there seems to be little else to suggest modifications along the lines we have been discussing. The well developed genal comb and pronotal comb, plus the fact that some of the few bristles on the thorax and one on the head are unusually short and stout, lead me to believe it is specialized in another direction, as indicated in Section B.9 below.

Of unusual interest are hystrichopsyllids which possess some of the typical attributes of nest-fleas but which nevertheless bear genal and ctenidial combs, e.g. *Stenischia*°. Thus, these fleas are characterized by: reduction of the eye, thorax (including loss of the pleural arch), and chaetotaxy; long, slender legs; development of heavy incrassations on the dorsal margins of the abdominal terga and ventral margins of the sterna, coupled with unusually lightly tanned median portions of these segments—all features associated with nest-fleas. Here too, in my opinion, the ctenidia are reduced, but the term is a relative one, in that what appears to be well developed combs in reality probably represents a marked diminution in the size and number of spines borne by their ancestors, or by related taxa such as *Nearctopsylla* Rothschild, 1915, which have much more pronounced combs. This point is considered further in Sections IV.C.2 and IV.E below.

3. PYGIOPSYLLID NEST-FLEAS. Amongst the pygiopsyllids, there are only very few instances where fleas seem to have assumed the nest-habit. One is *Choristopsylla tristis*° (Rothschild, 1900), which, even more than other members of its genus, has reduced chaetotaxy (essentially only 1 row of bristles on abdominal terga and those very slender); long slender legs, with metatarsus I particularly long; the pleural arch so reduced as to be essentially absent; lateral metanotal area small, etc. Remarkable parallel developments between this flea and those of fleas of Nearctic flying-squirrels (and their hosts too) are mentioned later. Two other pygiopsyllids which are likely candidates, despite the presence of a pleural arch, are the monotypic *Lycopsylla* Rothschild, 1904 (Australia and Tasmania, on wombats) and *Notiopsylla* Jordan & Rothschild, 1914 (2 species, 1 ex procellariiform sea-birds; the other apparently from a parakeet that spends most of its time on the ground; both on sub-antarctic islands). Both of these genera are combless, a highly unusual condition amongst pygiopsyllids, and the lateral metanotal area is narrow. However, *Notiopsylla* is clothed with many fine hairs, suggesting it may spend some time on the host as well as in the burrows. The scanty records indicate this is so for *N. kergue-*

lensis (Taschenberg, 1880), but *N. enciari* Smit, 1957 is apparently known only from a very few specimens and hence data are lacking.

Lycopsylla shows marked reduction of chaetotaxy (both in numbers and size of bristles), but the pleural arch is better developed than in known nest-fleas. As will be shown, the size of the pleural arch is correlated with jumping ability, and since fleas of large mammals tend to be excellent jumpers (e.g. *Ctenocephalides* Stiles & Collins, 1930), and the wombat grows to a size of about 1200 mm in length and about 800 mm in height (more than 20 inches tall), it is not surprising that this flea does not show much reduction of the thorax

4. CERATOPHYLLID NEST-FLEAS. Nest-fleas occur in the Ceratophyllidae too, although they are of much less frequent occurrence than in the Hystochopsyllidae. Among the classic examples are a relatively few species of the large genus *Ceratophyllus* Curtis, 1832, such as the Nearctic *C. arcuegens*° (fig. 90), and the Palaearctic *C. rusticus* Wagner, 1903, *C. caliotes*° Jordan, 1937 and *C. orites*° Jordan, 1937, in which there is reduced chaetotaxy, loss of the pleural arch, development of slender legs, etc. (Holland, 1952; M. Rothschild, 1969). *C. delichoni*° Nordberg, 1935, also belongs in this category, as can be seen from Smit's excellent re-description (1956). These fleas parasitize martins and cliff swallows, but there are also other species of *Ceratophyllus* that infest these particular birds, e.g. *C. styx* (fig. 91), and yet which lack most or all the morphological modifications of the *C. arcuegens*-group, as can be seen by comparing figs 90 and 91. This is discussed below, when it is pointed out that these bird-nest fleas have well developed eyes, unlike the case in fleas of mammal-nests.

Perhaps the most remarkable bird-flea is the Antarctic *Glaciopsyllus antarcticus*° Smit & Dunnet, 1962, which lives in the nest of the snow-petrel, often under many feet of snow (Murray et al., 1967). This flea is so specialized that it has not only lost the pleural arch but the pronotal comb as well (and is thereby unique in the family), and shows the reduced chaetotaxy, slender legs and other nest-flea features, but here again the eye is large. Amongst ceratophyllids of mammals that seem to be nest-fleas, may be mentioned *Syngenopsyllus*° Traub, 1950 (Indo-Malaysian), *Libyastus*° Jordan, 1936 (African), *Tarsopsylla*° Wagner, 1927 (Holarctic), all of which are fleas of tree-squirrels (or their nests) and *Hollandipsylla*° Traub, 1953, from a Bornean flying-squirrel. I believe that to a considerable extent the following ceratophyllid fleas spend much of their time in the nest rather than on the host, viz., the 2 species of *Opisodasys* which parasitize flying-squirrels, *O. pseudarctomys*° and *O. vesperalis* (but not the rest of the species of *Opisodasys*, which infest tree-squirrels and *Peromyscus*); the dormouse-flea, *Myoxopsylla*° Wagner, 1927; the Mexican *Pleochaetis paramundus*, which is a *Neotomodon*-flea (but not the remaining 22 species of *Pleochaetis*, which infest primarily *Peromyscus*); and the Palaearctic marmot-flea *Callopsylla dolabris* (Jordan & Rothschild, 1911).

The ceratophyllid nest-fleas, especially those of mammals, are not as modified morphologically as are the bulk of the hystrichopsyllids, etc. However, all of those listed, save *P. paramundus* and *C. dolabris*, lack the pleural arch, but in the last 2, the arch is smaller than in their relatives, and the latter especially show other thoracic changes, such as a narrowing and deepening of the lateral metanotal area. All tend to have reduced eyes and have fewer and thinner bristles; and more slender and elongate mouthparts and legs; and a narrower metepimere (except for *P. paramundus*), than do their allies which infest the fur of their hosts. The more specialized thoracic differences may be seen by comparing fig. 87 (*O. hollandi*, a fur-flea of diurnal tree-squirrels) and fig. 88 (*O. vesperalis*°). The maximum degree of relevant differentiation in the family may be seen by contrasting the head and thorax of *C. arcuegens*° (fig. 90) with that of *C. styx* (fig. 91). There is an odd species ascribed to the Ceratophyllidae which may prove to be a nest-flea, namely *Brevictenidia mikulini* (Schwarz, 1960), the sole representative of the genus (and which I have not seen). This is characterized by a pronotal comb of "vestigial" widely-spaced, acuminate spines which are less than ½ the length of the pronotum. The elongate palpi, the very small eye, and reduced chaetotaxy shown in the published figures (Liu & Li, 1965) parallel the modifications indicated above. There is some doubt about whether this really is a ceratophyllid or leptopsyllid.

5. LEPTOPSYLLID NEST-FLEAS. There are few nest-fleas known in the Leptopsyllidae, but these exhibit the same tendencies. Thus, *Brachyctenonotus*° Wagner, 1928, a monotypic genus parasitizing mole-rats in south central Asia, not only lacks the pleural arch and has a very reduced eye, but its pronotal comb consists of extremely short and broad spines. Allied to *Brachyctenonotus*° is the monotypic genus *Calceopsylla*° Liu, Wu & Wang, 1965, which judging from the figures and English summary of the original description (Liu, Wu & Wang, 1965), is a typical nest-flea since the eye is absent, the palpi elongate, the pronotal comb markedly reduced, the pleural arch missing, the abdominal spinelets absent, etc. The spines of the comb are narrow, very short and widely spaced, as in the former genus. *Phaenopsylla* Jordan, 1944, *Hopkinsipsylla* Traub, 1963 and *Paradoxopsyllus microphthalmus* Ioff, 1946, although possessing the pleural arch, conform to the picture that is now familiar through repetition.

An instructive stage in the development towards the nest-flea habitus is seen in *Amphipsylla marikovskii* Ioff & Tiflov, 1939. In ordinary species of *Amphipsylla* Wagner, 1909, the eye is quite small; there are about 20 spines (total) in the pronotal comb, the pleural arch is well developed, the lateral metanotal area is relatively broad, and the false combs of bristles on the pro- and metatibiae are generally prominent. In *A. montana* Argyropulo, 1946, for example, it may be noted that spines numbers 2–4 of the pronotal comb (fig. 105) are fairly straight and number 3 is more than 5 times as long as broad; the tanned margins of the pleural arch (PL.A.) extends well below the apex of the pleural rod (PL.R.); the gap between the arch and the tip of the rod exceeds the girth of the dorsal part of the rod; the lateral metanotal area (L.M.) is only about 1·3 times as long as tall and scarcely extends beyond the pleural rod; there is a false comb of 8 short, stiff, straight, somewhat spiniform bristles on the protibia (fig. 103) and one of about 6–8 such modified bristles on the metatibia (fig. 104). In contrast, in *A. marikovskii*, the eye is almost vestigial; there are only about 16 spines in the pronotal comb (fig. 100), spines numbers 3–5 are dorsally concave and relatively broad, e.g. number 3 is about 3·8 times as long as broad at the base; the pleural arch (PL.A.) is greatly reduced, viz., it is very small and compact, scarcely broader than the apex of the pleural rod (PL.R.) and almost contiguous with it; the lateral metanotal area is somewhat narrowed, viz., about 1·5 times as long and extends well caudad of the rod; the false comb on the protibia (fig. 101) consists of only 4 straight bristles and that of the metatibia (fig. 102) of but 3 bristles and these are inclined more ventrad than in unmodified members of the genus.

An earlier step in this evolutionary trend is illustrated by fig. 94, showing the head and thorax of *Ophthalmopsylla* (*Eremedosa*) *celata* Traub, 1965 compared with that of *O. jettmari* Jordan, 1929, which is not a nest-flea (fig. 95). It is apparent that in *O. celata*, the eye is greatly reduced, the bristles are far fewer in number and are significantly more slender; the lateral metanotal area (L.M.) and metepimere (MTM.) narrower, the pleural arch (PL.A.) smaller and narrower, etc. There are fewer spines in the pronotal comb, but here *O. celata* has not progressed as far as *Phaenopsylla* (vide fig. 80), which has also become more specialized in other respects, viz., the eye is vestigial.

6. Pulicid Nest-Fleas. Nest-fleas are rare in the Pulicidae, and it seems highly significant that the only such mammal-flea known to me, *Xenopsylla papuensis*°, a parasite of *Pogonomys* in New Guinea, conforms closely to the pattern and may be unique amongst the 70 described species in the genus in lacking a true pleural arch. Actually, the pleural arch is present in vestigial form (PL.A.(?)), arising from the ventrocaudal angle of the lateral metanotal area (L.M.), but it is extremely short and narrow, and is virtually contiguous with the top of the pleural rod, especially in the male. Like all *Xenopsylla* Glinkiewicz, 1907, it is combless, but as can be seen by comparing fig. 92 with fig. 93 (a New Guinean specimen of the related *X. vexabilis*, a fur-parasite of rats), the eye is absent in the former species, instead of being quite well developed; there are fewer bristles on the head and on the metepimere (MTM.), e.g. 2 4 instead of 5–5; the bristles in general are distinctly narrower; and MTM. is relatively narrow.

In the California pulicid flea of sea-birds, *Actenopsylla suavis* Jordan & Rothschild, 1923, there is a very small pleural arch and the lateral metanotal area is narrow, recalling the condition in some other fleas of sea-birds, and the accompanying reduction of the eye (fig. 99) and the chaetotaxy suggest that the flea spends much of its time in the nest-habitat of its host (*Ptychorhamphus*), which is in burrows in the ground. It seems significant that this flea, and its ally, *Ornithopsylla laetitiae* Rothschild, 1908, the only bird-fleas in the group, are likewise the only members of the tribe lacking genal and pronotal ctenidia. The latter is also a flea of sea-birds (*Puffinus*), and has been found in their nests as well as on the bodies of the hosts, and is modified along somewhat similar morphological lines as *Actenopsylla* Jordan & Rothschild, 1923. However, the straight frontal margin of the head of *Ornithopsylla* Rothschild, 1908 and the somewhat larger eye, lead me to believe that it is not as much of a nest-inhabitant as the former.

7. Chimaeropsyllid Nest-fleas. The small family Chimaeropsyllidae is limited to the Ethiopian Region and primarily to South Africa. The majority of the

species of the largest genus, *Chiastopsylla* Rothschild, 1910 (xi.2) are definitely stated to be nest-fleas, e.g. all members of the *numae*-group and especially *C. numae* (Rothschild, 1904) and *C. quadrisetis* de Meillon, 1930, and at least 5 of the 8 species in the *mulleri*-group, namely those found in the nests cf *Otomys unisulcatus*, the Karoo rat (de Meillon, Davis & Hardy, 1961; Haeselbarth, 1966). *Chiastopsylla* reminds one of *Anomiopsyllus*° because of the diminutive size of the species and the marked reduction in chaetotaxy. However, unlike the latter, *Chiastopsylla* does have combs, both genal and pronotal. Significantly, though, the pronotal comb is greatly reduced and usually consists of only 5–7 short spines per side, and the genal comb at most consists of 2 spines, and at times only 1, and may be missing altogether, as in *C. pitchfordi* Ingram, 1927. Such variability of numbers of spines suggest the structures are in the process of elimination in the course of evolution. The maxillary palpi are relatively long and thin, and in *C. pitchfordi* extend to near the apex of the trochanters, and the eye is vestigial. The pleural arch is present, but is very small. The known ultimate in this line of development in the family is in the monotypic genus *Praopsylla* Ingram, 1927, which lacks combs entirely, and in which the eye is so reduced that it is represented by a mere small tanned patch. The head has an unusual subconical appearance at the frontal angle due to the anterior excision of the ventral margin, a configuration that can be seen in some other nest-fleas, e.g. *Eopsylla*° (i.2) and *Conorhinopsylla*° (i.2), (fig. 86) while the mouthparts are elongate, extending beyond the apex of the fore trochanters, the pleural arch is very small, and there is but a single row of bristles, and even the bristles on the hind tarsi are unusually short. Superficially *Cryptopsylla* de Meillon, 1949 resembles these nest-fleas, but consideration of this is best deferred.

8. Rhopalopsyllid Nest-fleas. Members of the family Rhopalopsyllidae are essentially Neotropical rodent-fleas, with a few exceptional members occurring in the subantarctic region or in southern U.S. and with some infesting birds or other hosts. Many new species, and perhaps undescribed genera, undoubtedly await discovery, for most of South America is still unexplored concerning fleas. None of the species bear true ctenidia (Traub, 1968) and one cannot discuss such modifications when considering nest-fleas. However, a number of forms exhibit reduced chaetotaxy (regarding numbers of rows, diameters), lengthened palpi and an unusually large (and variable) number of palpal segments, e.g. *Ectinorus polymerus* Jordan, 1942 and *Dysmicus barrerai* (Jordan, 1939). It therefore seems significant that Jordan (1942) cites these as being found in the nests of their hosts (*Octomys*), or, in the case of the latter species, flourishing there. The features of other related taxa suggest they too may be nest-inhabitants to a degree, and for example, de Meillon (1952) states that "*Parapsyllus* . . . is essentially a nest-flea", but on the whole too little is known about the fauna, and their habits, for further discussion.

9. Differences in degree of the Nest-flea Habitus. It is therefore clear that the development of the nest-flea habitus and habit has occurred independently many times within the Order, viz., in at least 7 families, and in 5 subfamilies of one of these, the hystrichopsyllids. However, it is emphasized that the degree of con-

vergence or differentiation varies. *Jordanopsylla* lacks combs but has a pleural arch; some have a short comb but no pleural arch; neopsyllids are quite small in size while the squirrel-fleas are of fair size, etc. It seems that some species, like *P. paramundus* (fig. 68), are relatively late entries in this line of development, and still may be found in fair number on the bodies of the host, and these tend to show a lesser degree of specialization by reduction, e.g. the eye is definitely smaller in *P. paramundus* than in other *Pleochaetis*, but it is not vestigial, and the pronotal spines are short as compared with the pronotum and are relatively quite broad, but the comb is not as modified as in *Strepsylla* (fig. 79) and *Epitedia* (fig. 77), etc. Other species of genera of nest-fleas have been extremely difficult to collect unless and until one has the opportunity to examine the nests of the hosts, as was the case with *Hopkinsipsylla* (Traub, 1963, 1965). This has also been the experience with *Tamiophila*, *Phalacropsylla* etc., while others have remained "rare" despite intensive collection of mammals in the endemic habitat, presumably because it has not been possible to seek or find the nest of the host, as happened with *Jordanopsylla* and the subgenus *Eremedosa*.

Certain genera of Siphonaptera possess some of the attributes of nest-fleas but have other characteristics which suggest that these fleas are not merely specialized to crawl about in the nest and feed on sleeping hosts. It appears that some of these species are progressing towards the nest-habit, while others may be evolving away from it, and these are herein referred to as *partial nest-fleas*. Such evolutionary manifestations are not surprising, since it seems logical to believe that the Order arose from a non-parasitic ancestor which lived in the nests of mammals or protomammals, feeding on organic debris, and later, perhaps, on scurf on the bodies of the residents, and gradually acquiring the facility to feed on the blood of what were by then their hosts. Development of the ectoparasitic habit was accompanied by the adaptations of making it more and more successful, e.g. flattening of the body, presence of rows of stiff backward projecting bristles or combs of spines; development of jumping legs (N. C. Rothschild, 1917; Ioff, 1929; M. Rothschild & Clay, 1952; Traub, 1966); modification of the flight mechanism into a device for leaping (Neville & M. Rothschild, 1967; M. Rothschild, 1969). It is believed that most (but not all) of the early fleas possessed many combs of spines and that most of these ctenidia have become vestigial or lost (at times with scarcely any trace) as the fleas developed other means of remaining safely on the host despite its exertions in running, or flying, or special efforts to destroy the flea by teeth, beak or claw (Traub & Barrera, 1966; Traub & Evans, 1967; Traub, 1968, 1969). Some of these new mechanisms include "false combs" of bristles to replace the true combs which had been lost (Traub, 1968). It therefore appears that the "specialization by simplification" (Hopkins & Rothschild, 1962) of nest-fleas is indeed just that, a series of modifications enabling the flea to return to a nest-existence, but in a manner superior to that of its forebears. However, in some instances, superimposed upon the model characterized by reduction of the combs and bristles, etc., are later or concurrent adaptations which enable the flea to remain on the host when it is active in the nest or burrow, or even outside, while running, leaping, gliding or flying.

An example of a taxon of fleas with such a "dual-purpose" set of modifications is the anomiopsylline hystrichopsyllid *Stenistomera*°, known from 3 species in the Nearctic deserts. Here the eye is vestigial and marked modification of the thorax accompanied the loss of the pleural arch (i.e. absence of the lateral metanotal area) and there is reduction in abdominal chaetotaxy (but one row of tergal and sternal bristles, and with intercalaries vestigial), while the legs are long and slender. However, this picture of a typical nest-flea is confused by features illustrating another evolutionary trend, which is exhibited in non-nest fleas representing such diverse taxa as some (but not all) species of *Jellisonia* Traub, 1944 and *Kohlsia*, which are ceratophyllids, and by the leptosyllids *Amphipsylla, Caenopsylla* Rothschild, 1909, *Ctenophyllus* Wagner, 1927, and *Peromyscopsylla* I. Fox, 1939, and by pygiopsyllids like certain *Metastivalius* Holland, 1969. These are the *combination* of: (1) A narrowed frontal region on the head (i.e. it is taller than long and often bullet-shaped); (2) A frontal margin that is somewhat flattened for the ventral half. (3) A row of frontal bristles bordering the anterior margin. (4) Tendency for bristles of the first row to be thickened near the base, or, somewhat spiniform. (5) Presence of a "false comb", i.e. a vertical row of single, short or stiff bristles, on the tibiae. (6) A full pronotal comb of many, narrow spines, with the lowest spine (or additional ones) extending over the vinculum. Modifications of the frontal margin of the head in this manner is deemed by me to be characteristic of fleas which become temporarily rather sedentary and cling to the host by hooking the marginal row of subspiniforms or thickened bristles onto the hairs while the flea abuts its head against the skin (Traub, 1968, 1969). It is noteworthy that in *Stenistomera*° only *S. alpina*° (Baker, 1895) exhibits all of these "secondary" features. In *S. macrodactyla*° Good, 1942, the first row of frontal bristles is not so marginal nor subspiniform; the tibial combs not so well developed, etc., while *S. hubbardi*° Egoscue, 1968 is intermediate. It would seem that *S. alpina*° is adapted both to feed on the host while it is in the nest and to cling successfully to the fur while the *Neotoma* is outside, where a fall from the host might mean death for a nest-flea, as stressed below (Section IV.C.2).

In the category of a flea apparently following two lines of evolution simultaneously, viz. specialization by reduction complemented by elaboration of existing structures, is the South African monotypic genus *Cryptopsylla* (xi.2). It superficially resembles the related *Praopsylla*, which presumably is a true nest-flea, in that there is no sign of a comb, but the eye is even more reduced—it is completely absent. However, there are significant differences in that the mouthparts are much shorter, there is a false comb of modified bristles on all the tibiae, and while there is but one row of abdominal bristles, these are unusually long. This is a flea of a burrowing rodent with mole-like habits, the bathyergid *Cryptomys*, and I believe the loss of the eye and development of unusually long bristles is characteristic of fleas of such hosts (i.e. *Dactylopsylla* Jordan, 1929 (iii.2) of Nearctic pocket-gophers; *Dinopsyllus* (*Cryptoctenopsyllus*) *ingens* (Rothschild, 1900) (i.4), a flea of the mole-rat *Bathyergus*). Such a coat of long thin bristles (coupled with marked reduction of the eye) is also seen in the 4 genera of fleas parasitizing *Aplodontia*, a North American rodent which spends much of its time burrowing. It seems likely that vestiture of this type not only may help the flea stay on its host while the latter brushes against the walls of its tunnels, and that the close proximity, great length and overlapping condition of the bristles also offer protection against the grains of soil that would otherwise dust and adhere to the flea in such an environment. Since *Cryptopsylla* not only has chaetotaxy of this pattern, but also is adorned with tibial combs, I believe it spends time on its host as well as in the nest.

Other examples of fleas which have some of the attributes of nest-fleas, but not many, and which have been collected in rodent nests are *Xiphiopsylla* Jordan & Rothschild, 1913 and *Coptopsylla* Jordan & Rothschild, 1908. *Xiphiopsylla*, a genus infesting primarily rodents in the Ethiopian Region, is sufficiently distinctive to be placed in a family by itself, and the features relevant to this discussion include a vestigial eye, long thin maxillary palpi, a short pronotal comb of short spines (and hence pronotum greatly exceeding length of spines); a reduced pleural arch (virtually vestigial in *X. hyparetes* Jordan & Rothschild, 1913); a narrow metepimere and fairly slender legs. However, there are 2 or more full rows of abdominal bristles on the terga, and the long bristles are remarkable in being sword-shaped, i.e. virtually straight from base to near apex instead of tapering in the usual way. The body surface is heavily sclerotized, reticulated, sculptured or microspiculose, and there often are dorsal incrassations on the terga. The body ornamentation and the densely tanned nota may be regarded as adaptations for protection against being crushed or caught by the host, but likewise would be of value when squeezing into crevices in the nest of the host, and the stiff bristles and reticulated surfaces would facilitate crawling into tight cracks and offer resistance to being pulled out therefrom. Similar incrassations are seen in some hystrichopsyllids like *Xenodaeria* Jordan, 1932 (Doratopsyllinae), *Rothschildiana* (Neopsyllinae), the rhadinopsylline *Stenischia* Jordan, 1932 and *Corypsylla* C. Fox, 1908, and are examples of convergence. *Rothschildiana* also bears comblike bristles on the sterna, and the body is rigid, with the surface spiculose. These specializations suggest it likewise hides in narrow apertures in the nest.

Coptopsylla likewise is the sole representative of a special family, and is a desert flea in the southwestern subregion of the Palaearctic Region. It is strongly reminiscent of true nest-fleas in the absence of any combs, in the extreme length of the palpi and stylets; the tall, narrow lateral metanotal area, and the presence of but a single row of abdominal bristles. However, there is a well developed pleural arch, a large eye and the bristles are long, and these indicate a flea that spends at least part of the time on an active host, and as we shall see, is a good jumper and is active in the daylight.

Additional points about fleas which might be nest-fleas to a degree will be deferred until a discussion of the absence of the pleural arch and the reduction of the eyes in Siphonaptera.

Inasmuch as so many of the nest-fleas have been indicated as having lost the pleural arch and possessing reduced or vestigial eyes, these points are discussed below, since other types of fleas are so modified as well.

C. The Pleural Arch of the Metathorax

1. Review of Taxa Lacking a Pleural Arch. The absence of the pleural arch of the metathorax in certain fleas (e.g. figs 85, 86, 90, 92) is of interest and significance and constitutes another good example of Convergent Evolution in fleas, since the condition occurs in a fairly large number of genera which are often unrelated, while close allies have normal pleural arches (figs 87, 91, 93, PL.A.) (Traub, 1953b). At times, only one or two members of a large genus are affected, e.g. *Xenopsylla*, and loss or marked reduction of this structure is known in at least 6 families (Hystrichopsyllidae, Pygiopsyllidae, Ceratophyllidae, Leptopsyllidae, Ischnopsyllidae and Pulicidae) although it is quite rare in the pygiopsyllids, leptopsyllids and pulicids. Further, fleas with this trait are found in a variety of habitats in widely separated geographic areas. Ceratophyllid squirrel-fleas with the thorax modified in this manner were listed by Traub (1950, 1953), viz.: *Tarsopsylla*°[9] (Holarctic), *Syngenopsyllus*° (Indo-Malaysian), *Libyastus*° (Ethiopian), the 2 species of *Opisodasys* Jordan, 1933 which parasitize Nearctic flying-squirrels, viz. *O. pseudarctomys*° (fig. 47) and *O. vesperalis*° (fig. 88) and the monotypic Bornean flying-squirrel flea *Hollandipsylla*°. A small minority of ceratophyllid bird-fleas lack the pleural arch (Holland, 1952; M. Rothschild, 1969) i.e. *Ceratophyllus arcuegens*° (fig. 90) and the 3 other martin and bank-swallow fleas mentioned above, as well as the notable Antarctic flea, *Glaciopsyllus antarcticus*°. The arch is likewise missing in the ceratophyllid dormouse-fleas *Myoxopsylla*° and in the leptopsyllids *Brachyctenonotus*° and *Calceopsylla*°. A leptopsyllid in which the arch is greatly reduced but still discernable is *Amphipsylla marikovskii*. Among hystrichopsyllids, most anomiopsyllines (e.g. *Anomiopsyllus*°, *Megarthroglossus*°, *Conorhinopsylla*°, *Callistopsyllus*°, *Stenistomera*° and *Eopsylla*°) lack the pleural arch (Traub & Tipton, 1951) as do nearly all rhadinopsyllines (e.g. *Rhadinopsylla*°, *Corypsylla*°, *Trichopsylloides*° Ewing, 1938, *Paratyphloceras*° Ewing, 1940, *Stenischia*° and *Wenzella*°). When present in this subfamily (*Nearctopsylla* Rothschild, 1915), it is very small and the associated pleural rod is abbreviated. In neopsyllines, the pleural arch is definitely reduced in *Phalacropsylla, Genoneopsylla, Delotelis, Epitedia faceta* (Rothschild, 1915), *Tamiophila* and somewhat less as in *Strepsylla, Meringis, Catallagia* and *Paraneopsylla* as compared to *Neopsylla.* Amongst ctenophthalmines, the arch is absent in *Agastopsylla*°. Among the doratopsyllines, *Idilla*°, a monotypic genus known from dasyurine and peramelid marsupials, is similarly modified.

The arch is absent in many ischnopsyllids (bat-fleas) i.e. *Thaumapsylla*° Rothschild, 1907, *Lagaropsylla*° Jordan & Rothschild, 1921, *Araeopsylla*° Jordan & Rothschild, 1921, *Nycteridopsylla*° Oudemans, 1906 (fig. 89), etc. and is greatly reduced in *Ischnopsyllus* Westwood, 1833, *Oxyparius* Jordan, 1936 and others. Amongst pulicids, *X. papuensis*° has a thorax essentially of this type (fig. 92), thereby differing from its many allies (e.g. fig. 93). This structure is much reduced in *Rhynchopsyllus* Haller, 1880 and *Hectopsylla* Frauenfeld, 1860, which are sticktight fleas infesting birds or bats, and is also very small in male *Tunga* Jarocki, 1838 and virtually absent in female *Tunga*. These particular sticktight and burrowing fleas are at times placed in the family Tungidae but are regarded by some as a subfamily of Pulicidae. *Choristopsylla tristis* is one of the few pygiopsyllids known to lack the pleural arch. Another is *Pygiopsylla celebensis* Ewing, 1924, represented by but one specimen extant and with unknown affinities and host relationships.

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[9] It is reiterated that the species which are marked ° in this article, lack the pleural arch.

Although the above review does not purport to be complete, it is clear that reduction of the thorax and loss of the pleural arch has occurred repeatedly and often sporadically throughout the Order, and without much regard for taxonomy. The important question is, what is the significance of this evolutionary development? Unless one wants to believe that an Order may have a built-in mechanism for the haphazard appearance of a single-type mutation or atavism, there ought to be a common factor or basis for such repeated but natural selection of an unusual trait. Moreover, the first possibility is ruled out since the loss of the pleural arch is accomplished in several different ways, as will be shown. In short, this trait should be adaptive or at least fit with known evolutionary principles, and in what follows an attempt will be made to demonstrate that this is indeed the case.

2. THE ADAPTIVE VALUE OF THE LOSS OF THE PLEURAL ARCH. A review of the list of fleas with this type of thorax, made in an attempt to determine the possible value of the modification, immediately leads to some generalizations. One is that virtually all have reduced eyes. However, the relatively few exceptions have unusually large eyes, so apparently that phenomenon is complex, and hence it will be treated later, separately, in Section IV.D.1. It is also evident that most of the names are familiar in that they were mentioned above as nest-fleas. Nevertheless, there is one glaring addition—the bat-fleas, and these provide a clue as to the function of the reduced arch, as shown below.

Various workers were impressed by the high incidence of the reduction of loss of the pleural arch in nest-fleas, and postulated that it was associated with the lessening or loss of the ability to jump well, or with sedentary habits (Traub, 1953). Apparently, the first direct statement to this effect was made by Holland (1952) when describing his new bird-flea, *Ceratophyllus arcuegens*. He noted that, like 3 Palaearctic members of the genus (out of the many *Ceratophyllus* known), this species lacked a pleural arch (fig. 90), and went on to state that because of the reduction of the legs and thorax, and as indicated by the "rather large and deep abdomen," this was "evidently a rather sedentary species . . . ; a crawler rather than a jumper." Earlier, without specifically mentioning the loss of the pleural arch, Holland (1949), in referring to *Tarsopsylla* , stated that "in spite of its long legs, [it] appears to be a rather sluggish flea." Smit (1953b) made similar observations regarding *Tarsopsylla*, but again without reference to the arch, declaring "It seems to be a general rule in fleas that the ones with long and slender legs are walkers and climbers rather than jumpers, while those with stout and relatively short legs seem to be the jumping champions". Johnson (1957) discussed various modifications of the lateral metanotal area and the pleural arch, and stated she believed the latter was "mainly an aid in jumping". Johnson also indicated that "prior loss of the pleural arch is somehow connected with incorporation of the lateral metanotal area into the notum or to its complete loss". Smit & Dunnet (1962) expressed the view that *G. antarc-*

ticus° was a crawling flea, a point that was verified later by field observations (Murray et al., 1967). Traub & Evans (1967) regarded the modifications of nest-fleas, including reduction in jumping ability, as adaptations for feeding on a quiescent or sleeping host, but the true significance of the loss of the pleural arch became clear only after the brilliant work of M. Rothschild and colleagues. The pleural arch of fleas was shown to be the site of a cap-shaped mass of resilin, "an elastic protein which stores and releases energy more efficiently than any known rubber, and which can deliver power faster than most efficiently contracting muscle." (M. Rothschild, 1969.) The pleural arch of fleas is homologous with the hinge-ligament of the wing of flying insects, which is situated on the top of the pleural ridge of scorpion-flies, locusts, etc., and consists of resilin (Neville & Rothschild, 1967). The latter authors referred to fleas as "insects that fly with their legs" since the jump is effected by a modified flight-mechanism. Reduction or loss of the pleural arch, then, can only be associated with lessened ability to jump.

What advantage from loss of the arch results to fleas like *Megarthroglossus*°, *Stenistomera*° or *Conorhinopsylla*° in a nest of *Neotoma* on the ground or in a rock-ledge, or *Callistopsyllus*° in an underground nest of *Peromyscus*? As already indicated, these fleas are seldom found on rodents away from the nest, presumably not only because they are morphologically and physiologically adapted for feeding on the host while it is resting or sleeping, but because they are so ill-fitted to escape falling off an active host or being killed by it. It seems eminently logical to believe that they are not equipped to survive the external environment outside the nest, and probably neither are the eggs nor larvae. Further, most of the species cited are desert-species, and it probably is no coincidence that a large proportion of nest-fleas are species infesting mammals living in xeric areas.

Bearing in mind that nest-fleas are essentially blind and keyed to living in the dark confines of the nest, it is clear that a nest-flea which was a good jumper might, in one leap, end up in an extremely hostile environment just a few inches away from the nest. Moreover, such a flea would be unlikely to find its way back. Darskaya (1955) noted that the desert-flea *Xenopsylla gerbilli caspica* Ioff, 1950 (ix.1) dies quickly if it misses in an attempt to attach to a passing host and fails to return to the burrow promptly. Since this is not a nest-flea, and is adapted to conditions at the burrow-entrance, it is no doubt hardier regarding environmental factors than a species attuned to the microclimate deep in the rodent nest. Another disadvantage to a nest-flea of being a good jumper would be the injuries sustained in leaping about blindly in closely confined quarters. A jumper would not be very likely to crawl within the relatively favourable runway of the host if it fell off the rodent, and instead would leap into an alien world. Thus, survival in the nest-flea would be most favoured in the poor jumper and natural selection would in time lead to the reduction and loss of the pleural arch so characteristic of nest-fleas. There is then, much more to the evolution of a thorax without a pleural arch than the mere "lack of need" for effective leaps in a species of flea living in underground nests.

The adaptive value of this development is further indicated by the fact that the loss of the arch is commonly seen in nest-fleas inhabiting nests or roosts at high altitudes, e.g. squirrel-nests on tall trees, bird-nests on cliffs or in banks, or in caves, or crannies in a tall cave where bats cling, or in holes where bats roost. As Dr Miriam Rothschild has pointed out in the lecture summarized by Neville & M. Rothschild (1967) a leap of 10-12″, the type readily accomplished by a flea with a well developed pleural arch, could carry an aerial nest-flea 100 feet down and away from the host it is dependent upon for the blood-meal necessary for nourishment and to prime egg-laying. The selective survival value of the modification of the thorax in such a nest-flea is apparent, particularly if it is faced with the problem of locating and attaching to its host in the dark, as in the case of bat-fleas and flying-squirrel fleas. However, fleas of volant and gliding hosts, or mammals living far above the level of the ground face a dilemma, because coupled with the need for restricted mobility there is the exacerbated problem of safely remaining attached to the host at such altitude (especially if it is volant). It is therefore not surprising that such fleas, lacking a pleural arch, have not followed the evolutionary path of fleas of underground nests and effected reduction of the combs, but instead, on the contrary, have developed supernumerary spines or combs. This is discussed below, in Sections C.3 and C.4.

The loss or reduction of the pleural arch and the resulting inability to jump well is also adaptive in other categories of fleas, e.g. the Antarctic flea *G. antarcticus*°. This flea lives in the nests of the silver-grey fulmar and the snow-petrel, amongst the rocks on the ground (for the former host) or in crevices (for the latter) (Murray et al., 1967). In the spring, the fulmar burrows to its former nest-site through the snow before it has melted, and the petrel also returns to its own individual nest-site. Incubation of eggs and rearing chicks takes 4 months, a period of warmth which is provided by the bird and which is obviously suitable, with respect to time and environment, for the life-cycle of the flea, because all stages have been found in the nest. An Antarctic flea of marine birds that was a good jumper could find itself in the sea, or exposed to extremely cold temperatures without a host. It is worth recalling that other fleas of marine birds have poorly developed pleural arches and are apparently poor jumpers

Of special interest are the hystrichopsyllids which seem to be nest-fleas by virtue of the reduction of the eye, thorax, and the number of bristles; loss of the pleural arch, etc. but which nevertheless have well developed ctenidia. In this group are insectivore-fleas like *Corypsylla*° (I.8) which possess a vertical comb near the frontal margin of the head which presumably hooks onto the hairs of the host as the flea abuts its head against the skin, as discussed by Traub (1968, 1969). The flattened frons and the vertical genal comb of the related *Stenischia*° suggest a similar habit. The question arises as to why such fleas, particularly *Corypsylla*°, whose ctenidia would seem to belie a true nest-existence, have lost the pleural arch and are such poor jumpers. In the first place, as is mentioned in Section IV.J below for *Corypsylla*°, and has been noted above in IV.B.2, for *Stenischia*°, there is reason to believe that such ctenidia are literally reduced as compared to those of relatives, and that they thus represent evolutionary tendencies shown by nest-fleas in general. Secondly, it may be that the peculiar vestiture of the head is an adaptation to stay affixed to the fur of a host while it is asleep in its home, and that these fleas are semi-sessile for hours and are indeed nest-fleas. In this connection, it should be noted that the "banded" abdomen of these fleas, with its incrassate and rigid margins alternating with a softer middle, coupled with marked reduction of obtrusive abdominal combs and bristles, is ideally fitted to enable the insect to squeeze into, and out of, tiny cracks in the nest without being hurt, just as the reinforced segmental margins compensate for the loss of protection offered by the bristles of ordinary fleas. (It is significant that nest-fleas of birds are also "banded" but the alternating tanned and relatively soft sections of the abdomen extend from front to rear.) It therefore appears that these rhadinopsyllines are nest-fleas, at least in part, but there seems to be a third factor in the loss of the pleural arch, and that is the adaptive benefit to fleas which spend much of their time in narrow burrows, such as in the case of *Corypsylla*°, which infest moles and shrews. The question arises as to why such fleas have lost the pleural arch. It is, of course, possible for such fleas to utilize their specialized vestiture while feeding on a host that is in the nest asleep, and that development of this habit led to a semi-sessile existence and concomitant loss of the arch. However, other explanations for the *Corypsylla*-type of habitus seem more plausible. Fleas that jump well (e.g. *Ctenocephalides*) can leap heights of 8–10 inches (Traub, 1964), while moderately good jumpers like X. *cheopis* (Rothschild, 1903) may ascend to heights of 3–4 inches (Traub, 1964). Moreover, fleas usually make a series of leaps in succession. It is obvious that not only is there no need for such ability in fleas that may hatch out in, or frequent burrows that are only about 1½ inches in height, but that the resulting forcible and repeated collision with the roof of the burrow could be disadvantageous to the species as well as to the individual. Shrews and other insectivores tend to establish runways above ground as well as below the surface, and limited ability to jump would restrict loose fleas to these particular sites, whereas otherwise they may end up in a micro-environment that is injurious or remote from any suitable host.

Support for this last-mentioned hypothesis is provided by a new species of *Stenischia*° from the Himalayas of W. Pakistan. Very few specimens of any of the other species of this genus are known, and hence their true hosts are in doubt. However, the Pakistani flea is a parasite of *Hyperacrius*, a small burrowing vole that only very rarely emerges from the underground. It seems logical that such a flea would be a poor jumper, just as it is not surprising that the *Palaeopsylla* of this mole-like vole bears ctenidia resembling those of *Palaeopsylla* of moles rather than those of shrews (Traub & Evans, 1967).

The presence or absence of a well developed pleural arch is also adaptive in the hypodermal, sticktight and semi-sessile fleas. Those, such as the pulicine *Echidnophaga* and *Spilopsyllus cuniculi* (Dale, 1878), which have to seek and infest an active, large host, and which are sessile only part of their lives, have well developed pleural arches, and are thereby fit for the vital "great leap forward" onto their host. The tungine burrowing and sessile forms, e.g. *Tunga*, in contrast, presumably have very little difficulty in finding and infesting their hosts at ground-level and remain affixed for life and have greatly reduced pleural arches. In the tungines, the evolutionary path has been towards suppression of the locomotory parts of the body (and even much of the limbs become resorbed after attachment or penetration), while the feeding and reproductive ends are hyperdeveloped. Marked reduction of the entire thorax has therefore reduced the size of the target of the host bent on destroying the stationary flea and, in hypodermal species, has diminished the volume of body that must penetrate the skin of the host. In the case of *Echidnophaga*, etc., however, the advantage of being a good jumper outweighed the possible assets of loss of the pleural arch.

3. HYPERDEVELOPMENT OF COMBS IN BIRD-FLEAS, BAT-FLEAS, ETC. LACKING THE PLEURAL ARCH. It has been stressed above that the loss of the pleural arch is apparently adaptive, whether in fleas of bats, birds, flying-squirrels, squirrels nesting in tall trees, or of hosts nesting underground or on the surface. It has also been noted that instead of showing a tendency towards the reduction of combs exhibited by fleas of underground nests, the fleas of bats, birds, flying-squirrels (and of nocturnal arboreal animals in general) display, on the contrary, a trend towards a significantly greater number of spines in the pronotal comb, and, in the bat-fleas, development of a series of true combs (vide fig. 98) or of false combs (Traub, 1968). These modifications likewise can be explained in terms of adaptations. As in the case of the bird-fleas in burrows on the faces of cliffs, and the squirrel-fleas in nests atop huge trees, bat-fleas face the hazards associated with heights, and substituting the facility to crawl and climb, for the ability to leap is advantageous to the individual and to the species. This is true especially in the case of eyeless bat-fleas and other fleas of nocturnal hosts, which would have less chance of locating their prey by a blind leap in the dark.

However, once on an active, agile, volant, gliding or leaping host, these fleas must solve the severe problem of maintaining their hold, regardless of whether the bird or mammal is perched, moving or trying to kill or remove them. A fall from such a height might not be fatal, or even injurious to a flea, but there would be little chance of finding a new and suitable volant or arboreal host on the ground, even if it were day-time and the flea could see. It is therefore to be expected that bird-fleas and bat-fleas have "supernumerary" spines in the pronotal comb as a result of natural selection (note figs. 89–91, and compare the bird-*Lentistivalius*, fig. 18 with the murid-one, fig. 16), and that many bat-fleas have fairly well-developed abdominal combs, or even ctenidia of false spines on the metathorax, or dorsal stiff, spine-like bristles forming a series of comb-like projections (Traub, 1968). Humphries (1966) independently came to the same conclusions about the adaptive value of the combs of bat-fleas. This same principle, it seems to me, also applies to the nest-fleas of arboreal squirrels, and this is why, although they lack the pleural arch, *Tarsopsylla* (fig. 8), *Syngenopsyllus* (fig. 3), *Libyastus* (fig. 13) (all ceratophyllids) bear a full complement of spines, instead of having a reduced comb. Although precise data on the habits of some of these squirrel-fleas are lacking, the scarcity of records on the host and their demonstrated presence in nests lead me to believe that the last two are nest-fleas and/or infest nocturnal or crepuscular hosts, as mentioned below (p. 340). In the case of *Tarsopsylla* (iii.1), Holland (1949), Smit (1953b) and Sakaguti & Jameson (1962) all cited it as a probable nest-flea, and its long, thin legs are also highly suggestive of a flea that crawls rather than leaps. It is noteworthy that the pronotal spines of these particular squirrel-fleas are somewhat narrower and relatively longer than in the active fur-fleas of diurnal arboreal squirrels like some *Orchopeas* (figs 29, 31), *Opisodasys* (figs 46, 48) and *Monopsyllus* (figs 62, 64). This is presumably an additional step in the line of development, leading toward the adaptations of fleas of the flying-squirrels next discussed.

4. HYPERDEVELOPMENT OF THE PRONOTAL COMB IN FLYING-SQUIRREL FLEAS, ETC. As indicated above, the fleas of flying-squirrels tend to have a greater number of spines in the pronotal comb than do other members of the same genus which infest diurnal, arboreal squirrels or other hosts, and the spines are narrower and relatively longer, e.g. the Nearctic *Opisodasys* (iii.1) of flying-squirrels (fig. 47, *O. pseudarctomys*° and fig. 88, *O. vesperalis*°) versus *Opisodasys* from diurnal tree-squirrels (figs 44, 87, *O. hollandi* and fig. 48, *O. enoplus* (Rothschild, 1909)). The Bornean flying-squirrel flea, *Hollandipsylla neali*° Traub, 1953 (iii.1) also has a comb of this type (about 22 narrow spines). These particular flying-squirrel fleas also lack the pleural arch, unlike their allies, while in another (Himalayan) ceratophyllid of flying-squirrels, *Macrostylophora fimbriata* (Jordan & Rothschild, 1921) (fig. 97), the pleural arch is reduced as compared to allies on ground-squirrels, e.g. *M. borneensis* (fig. 96) and the pronotal comb likewise has a fuller complement than that seen in fleas of diurnal tree-squirrels (cf. fig. 7 versus fig. 14). A similar condition can be seen in comparing the ctenidium of a *Monopsyllus* from flying-squirrels (fig. 58) (iii.1) with one from ordinary tree-squirrels (figs 62, 64). The pleural arch of *M. argus* (Rothschild, 1908), from flying-squirrels, is also significantly shorter and narrower than in the *Monopsyllus* from tree-squirrels like *M. vison* (Baker, 1904). The Mexican *Orchopeas bolivari* Barrera, 1955 (New Combination) (iii.1) is believed to be a flea of flying-squirrels, and also shows this tendency (especially in the female), but to a lesser degree, perhaps because it is a recent association.

The same trend is seen in *Myoxopsylla*°, which are parasites of dormice, and although there are no known members of the genus occurring on other hosts which could be used for comparison, the comb extends more ventrad and has more spines than in related taxa, and the spines are also narrower. In *Monopsyllus sciurorum* (Schrank, 1803), which, despite its name, is a dormouse-flea, this same tendency is evident regarding a fuller comb and spines that are narrower in breadth and greater in number, as can be seen by comparing fig. 60 with the *Monopsyllus* of tree-squirrels shown in figs 62 and 64. It has been pointed out (Traub, 1969) that the fleas of nocturnal arboreal animals characteristically have a relatively large number of spines and that the comb descends sufficiently ventrad over the pronotum to reach or extend below the level of the third vinculum, while the lower spines are oblique in inclination, e.g. *Muesebeckella* Traub, 1969 (ii.1), *Acanthopsylla* Jordan & Rothschild, 1922 (ii.1), *Pleochaetis ponsi* Barrera, 1955 (iii.1), *Kohlsia keenani* Tipton & Mendez, 1961 (iii.1). *Tarsopsylla coloradensis*° (Baker, 1895) has a comb of this type, and from the figures cited, it can be seen that the comb of the *Opisodasys* of flying-squirrels and the other fleas of such crepuscular hosts approach this condition.

In the case of fleas of arboreal, nocturnal hosts, as with bat-fleas and fleas of nests atop tall trees, the pressures of natural selection would aid fleas that were crawlers, not good jumpers (hence the loss or reduction of the pleural arch), and/or which had an elaborate pronotal comb that would help them latch onto and retain a hold on a gliding or highly active host operating in the night, usually at heights that would offer little chance of survival for a flea that was dislodged. It therefore is not surprising that the end-result in such fleas is a pronotal comb which superficially resembles that of bird-fleas because of "supernumerary" spines, but which differs in essential details as noted above and elsewhere (Traub, 1969).

Of special interest and relevance in this discussion is the remarkable monotypic genus *Scolopsyllus* Méndez, 1968, the only member of the family Rhopalopsyllidae having a pronotal comb. The enormously significant feature about this unique pronotal comb is that it consists wholly of false spines, paralleling the condition of the "false helmet" on the head of *Smitella* Traub, 1968. In these instances the spine-like structures arise from definite setal bases, instead of directly from the integument as in the case of true spines, and similar false combs have been noted as occurring on other parts of the body in other taxa (Traub, 1968). That author, writing before the discovery of *Scolopsyllus*, pointed out that such false combs function as regular ctenidia but suggested that they are *not* substitute mechanisms for true combs which have been lost in the course of evolution, since they occur on parts of the body which apparently have never borne true combs in the forebears of those particular taxa. Accordingly, he predicted that a rhopalopsyllid might be found with a well developed comb of modified bristles on the pronotum, and went on to state that "if a pronotal comb of specialized bristles were found to occur, it would be in a flea secondarily adapted to bank- or tree-nesting birds or else in a parasite of a nocturnal arboreal mammal." Now that a rhopalopsyllid has been discovered with such a ctenidium, it may be significant that the false comb extends down over the vinculum, analagous to the case of fleas known to infest arboreal nocturnal hosts as mentioned above. The true host of *Scolopsyllus* is not yet known, the seven existing specimens having been collected from three species of *Oryzomys* or from *Reithrodontomys mexicanus.* Méndez (1968) believed that "Factors related to the micro-habitat of the flea on the host-pelage rather than the habits of the rodent or climatological conditions, are perhaps responsible for such modifications." It seems to me, however, that the habits of the host account for the evolutionary development in *Scolopsyllus*, and that this comb is another instance of the adaptive mechanisms mentioned above as being typical in fleas having a special need for a device to help them fix on to a very active nocturnal or volant host.

The only fleas of arboreal squirrels which show a marked tendency towards a reduction in the number of spines in the pronotal comb, accompanied by an increase in their breadth, are those which are highly modified as true nest-fleas like some *Megarthroglossus*°, *Conorhinopsylla stanfordi*° Stewart, 1930 and *Epitedia faceta.* It seems significant that these are fleas of diurnal squirrels that nest in fairly short trees or else live in tree-holes near the ground surface. It may also be relevant that each of these genera include species which are nest-fleas of ground-dwelling Peromyscini. Hence the adaptation to squirrel-nests may be a secondary or later development. The nest-fleas like *Libyastus*° and *Syngenopsyllus*° which have a fuller complement of spines, as mentioned above, infest squirrels living in nests in very tall trees. Moreover, it may turn out that the true hosts of these little-known fleas are nocturnal or crepuscular, especially in the case of *Syngenopsyllus*°. (It may be that *S. calceatus*° (Rothschild, 1905) is really a flea of flying-squirrels.) Regardless, the coupling of the comb of this type with the loss of the pleural arch is adaptive, as indicated. Similarly, even if *Tarsopsylla*° were a nest-flea of *Martes* (the fisher and martens) rather than of tree-squirrels, as records for at least the North American form suggest is possible, the argument is still valid, for the various species of *Martes* are nocturnal and largely arboreal. The possibility also exists that *Tarsopsylla*° is a nest-flea of flying-squirrels and if true, this would reinforce the above theories.

5. Convergence in Vestiture in Unrelated Fleas. That the above hypothesis about the evolutionary changes in the pronotal comb of fleas of flying-squirrels is correct is indicated by the modifications shown by the Australian *Choristopsylla tristis*°, one of the very few pygiopsyllids which lacks a pleural arch. Here we have the extraordinary case in which both parasite and host resemble, in important features, Nearctic species which are utterly distant phylogenetically and geographically. *C. tristis*° is a flea of *Petaurus*, a sugar-glider, a marsupial that looks and acts like a flying-squirrel (and, of course, there are no sciurids in the Australian–New Guinean area). Moreover, the flea exhibits reduced chaetotaxy, not only as compared with allied genera but also regarding *C. ochi* (Rothschild, 1904) (which has a very small pleural arch). The pronotal comb of *C. tristis*° bears about 10 narrow spines per side, resembling that of the ceratophyllid *Opisodasys vesperalis*° (fig. 88), a Nearctic nest-flea of flying-squirrels, but there are further and surprising parallels with nest-fleas of arboreal sciurids. For example, in *C. tristis*° there are 4 pairs of stout lateral plantar bristles on the last tarsal segment, with a mesal (ventral) pair in between the first pair and fully in line with them. (The mesal pair is in reality the true basal pair which has become displaced apicad and shifted towards the mid-line.) Thus, there is a total of 5 pairs of stout plantars in all. Ceratophyllids nearly always have 5 pairs of plantar bristles, and squirrel-fleas (and many others in the family) tend to have the first pair displaced somewhat mesad. However, the great majority of pygiopsyllids have 6 pairs, and the first pair is proximad of the second and only slightly moved toward the mid-line, e.g. *Acanthopsylla*. In *Bradiopsylla* Jordan & Rothschild, 1922, which is more closely related to *Choristopsylla* Jordan & Rothschild, 1922, there are only 5 pairs, but all are fully lateral. Even in *C. ochi*, which agrees with *C. tristis*° regarding displacement of the first pair, the third pair is somewhat shifted mesad, as in most members of the family, and there is also the customary dorsal pair of thin bristles on this segment, which *C. tristis*° lacks. *C. tristis*° is highly different from the general pygiopsyllids in another significant respect, and thereby also agrees with the *Opisodasys* of flying-squirrels in a trait that is highly unusual in the Ceratophyllidae—the first segment of the metatarsus is exceptionally long, being subequal to the tibia in length. In fact, the length of that segment approaches the condition in *Tarsopsylla*° (Holarctic squirrels or nests), which is almost unique in that the length of this segment I exceeds that of II–IV combined. (Liu & Li (1965) report that *Brevictenidia*, a monotypic genus of squirrel-fleas, resembles *Tarsopsylla*° in this respect.) Moreover, the relative length of metatarsus I in *C. tristis*° is significantly greater than that even in *C. ochi*, indicating specialization. The eye of the

former species is somewhat larger and better developed than in the latter (although still small), but it is equivalent to that of the *Opisodasys* of flying-squirrels (though ventrally excised instead of being entire).

Such parallels as those cited for the tarsi strain the credulity as being *bona fide* examples of convergence, but the precedent for such an extraordinary development exists in the Order, namely the shifting towards the mid-line of the third pair of plantar bristles of the apical tarsal segment, which occurs in 2 unrelated genera of bird-fleas, *Dasypsyllus* Baker, 1905 (iii.1) and *Ornithophaga* Mikulin, 1956 (iv.2) (Holland & Loshbaugh, 1958). Similarly, in the pygiopsyllid bird-flea, *Lentistivalius insolli*, the third pair of plantars is displaced to a greater degree than in the mammal-infesting species of the genus. The same tendency is seen in some other (not all) pygiopsyllid bird-fleas known to me.

An analogous shifting in the tarsal plantar bristles of bird-fleas has been noted earlier by Jordan amongst pulicids (1926) and cited as remarkable examples of convergence. In the tribe Spilopsyllini there are 3 genera (10 species) infesting mammals and all are combed, while 2 combless, monotypic genera parasitize sea-birds. In the mammal spilopsyllines the fifth tarsal segment bears 4 pairs of lateral plantar bristles of which the third pair is proximad of the middle or at the mid-line. However, in the bird-fleas, in *Ornithopsylla*, the third pair is shifted distad, whereas a similar trend is shown in the male of *Actenopsylla suavis* (shifted distad in mesotarsus and absent in the metatarsus) and the female has only 3 pairs on all legs. The case in the Xenopsyllini is more thought-provoking, for a similar development is seen only in the two *Xenopsylla* which occur on birds instead of rodents. *X. trispinus* Waterston, 1911 which infests *Petrochelidon* swallows in South Africa, is unique in that the third pair of lateral bristles on each side of segment is much nearer to the fourth pair than to the second. In *X. gratiosa* Jordan & Rothschild, 1923, a flea of *Puffinus*, a petrel, the third pair on the metatarsus gives the impression of being absent since one member is generally missing and the other displaced apicad and simulating a pre-apical plantar bristle (which are smaller and thinner than the laterals). On the other legs, in this species, both members of the third pair are shifted apicad and towards the mid-line. Thus, these bird-*Xenopsylla* exhibit a shift in the position of the third pair of tarsal bristles which Jordan (1926) alluded to as "crowding towards the apex," or else have eliminated these bristles. In all the mammal-*Xenopsylla* there are 4 pairs of lateral plantar bristles and the third pair is equidistant from the second and fourth. It is of interest that, as M. Rothschild & Clay (1952) have pointed out, the kittiwake flea, *Mioctenopsylla arctica* Rothschild, 1922 (iii.1) although a member of another family, also shows a tendency towards "a weakening and loss of tarsal bristles at least in the hind-tarsus."

Holland & Loshbaugh (1958) in remarking on analogous tarsal modifications in *Ornithophaga* (iv.2) and *Dasypsyllus* (iii.1) state: "If this is a case of adaptive evolution it is surely a remarkable one, and the survival advantage of such a character is not apparent to the authors." My feelings are similar, but since we are now learning to appreciate that so many seemingly insignificant structural modifications of fleas do have meaning or function, perhaps the tarsal changes likewise do. However, Jordan (1926) offered another explanation for the tarsal modification in the bird-pulicids. He pointed out that the "normal number of plantar bristles in Siphonaptera is 5 pairs; that is evidently the ancestral number, some genera having acquired more such bristles, many others having lost some of them." In the Spilopsyllini the trend has been to 4 pairs and hence "the tendency towards reduction already exists in the tribe." Jordan suggests that a "strong change in habit (or environment)" such as adaptation to birds as hosts "affects the growth and division of the chromosomes, rendering them unstable" and, in effect, this enhances the already existing genetic tendency towards modification of the plantar bristles. In short, the tarsal changes are unrelated side-effects that accompany the switch to a bird-host. Perhaps this is so, but certainly the many other modifications herein noted for bird-fleas and nest-fleas, etc. are apparently adaptive.

The fleas characteristic of *Aplodontia*, the sewellel or "mountain beaver" of the Pacific Coastal areas of North America, are instructive concerning several of the points that have been discussed, ranging from parallels in vestiture, to modifications suggestive of nest-fleas, shown by one species in particular. Three of the 4 *Aplodontia*-fleas: *Paratyphloceras oregonensis* Ewing, 1940, *Trichopsylloides oregonensis*° Ewing, 1938 and *Hystrichopsylla schefferi* Chapin, 1919, are hystrichopsyllids, and the first two belong to the Rhadinopsyllinae and the third is in the nominate subfamily. The fourth species, *Dolichopsyllus stylosus* (Baker, 1904) is a leptopsyllid in a unique monotypic tribe. In many respects the 4 species are as diverse as their generic names and taxonomic positions suggest, but they all agree in being very large, eyeless fleas, heavily clothed with a large number of very long, thin setae, and hence are remarkably similar in configuration (and thereby also resemble other fleas infesting burrowing mammals, as we have seen). The combed fleas of subterranean mammals like pocket-gophers and *Bathyergus* and *Aplodontia* (which not only digs well but spends most of its time in burrows) share another feature, and that is that the spines of the pronotal comb are unusually long and narrow, closely appressed and greater in number as compared to the condition in their relatives. The same tendency towards supernumerary, long, thin bristles and spines is seen in mole-fleas as compared to shrew-fleas, viz., the genus *Palaeopsylla* (Traub & Evans, 1967). It does not seem to have been noticed before, but there seems to be a definite correlation between the possession of a pronotal comb with many, narrow, close-fitting spines and chaetotaxy characterized by a plethora ot long fine bristles. Thus, this is true not only for the fleas of burrowing hosts, but also for all the combed bird-fleas, their highly polyphyletic origin not withstanding. (As has been pointed out by Traub (1966) the trait of unusually fine setae is found not only in bird-fleas as compared to mammal-fleas, but also in Mallophaga, cimicid Hemiptera and hippoboscid Diptera which infest both kinds of hosts.) This suggests that the ctenidial and chaetotaxic modifications may be adaptive and are associated with the pelage of the hosts at the site of infestation. Moles, pocket-gophers, *Aplodontia*, etc. have very fine, dense fur, at least on much of their bodies and the pinnules of certain feathers are also delicate and it therefore seems likely that the vestiture of these fleas has been tailored by the processes of selection to fit that of their hosts, but direct or quantitative observations have not been made insofar as concerns these particular fleas and animals. (Humphries (1966) in his fine paper on the function of combs, mentioned a bird-flea, but limited his studies to fur.)

In the case of the fleas of burrowing mammals there is another factor that merits further consideration concerning this condition of close-knit, lengthy fine hairs or spines which extend from one segment well onto the succeeding one. Such fleas infest hosts which are covered with earth and dust, and vestiture of this type must be useful in preventing such minute debris from slipping under the extensions of the terga and sterna. Fleas of other genera, when collected from mice covered with dirt in a trap, not infrequently have grains of soil imbedded under the overlapping segments. Many kinds of birds deliberately and frequently dust themselves in an action interpreted as aimed at reducing the itching caused by lice and other ectoparasites, and hence the same selective factor may be at work here in producing fleas with such modified vestiture. We lack sufficient data on the habits of birds and the infestation-rates of fleas to evaluate this hypothesis.

One of the *Aplodontia*-fleas, *Trichopsylloides*° has some of the characteristics of nest-fleas. Thus, it is essentially a *Rhadinopsylla*° which has lost its genal comb; and the pronotal comb does not extend down as far ventrad as in the other *Aplodontia*-fleas, and the spines are somewhat broader; there is no trace of a pleural arch; the legs are long and thin, etc. The only feature that suggests other habits is the chaetotaxy and the combination indicates that *Trichopsylloides*° is another instance of a nest-flea that can remain on the host when it leaves its nest.

6. MORPHOLOGICAL CHANGES IN THE THORAX ASSOCIATED WITH LESSENED JUMPING ABILITY IN FLEAS. In the Discussion thus far, reduced ability to jump has been shown to have adaptive value in many groups of fleas, ranging from bird-fleas and fleas of arboreal, nocturnal mammals, to fleas in nests underground. Methods of accomplishing this result are now considered.

Although the pleural arch has been reduced or lost in many instances and in a variety of taxa throughout the Order, a variety of mechanisms have been employed to achieve the conversion from a good jumper to a poor jumper or crawler, demonstrating that the term Convergent Evolution is an especially apt one in this case. In fact, the polyphyletic origin of the arch-less metathorax is apparent at a glance at figs 85–93, without recourse to the taxonomic characters used in systematics which placed the illustrated fleas in 5 families. This is not to say that representatives of each family modified the thorax in a manner that is characteristic of the family, for there are many variations on the thoracic theme in any one taxon (compare figs 85 and 86), and even in one genus there may be bewildering assortments (i.e. *Rhadinopsylla*). Fleas with a well developed pleural arch (PL.A.), and hence which are good jumpers, are shown in fig. 87 (*Opisodasys hollandi*) (iii.1) and fig. 91 (*Ceratophyllus styx*) (iii.1) and one with a fairly well developed one (*Xenopsylla vexabilis*) (ix.1) is illustrated in fig. 93. In such fleas, the resilin which provides the power-motif for the leap, is housed under the arch, above the apex of the pleural rod (PL.R.). Fleas lacking the pleural arch have no housing for resilin and hence are poor jumpers. Two members of the first two genera are in this category, and are illustrated in fig. 88 (*O. vesperalis*°) and fig. 90 (*C. arcuegens*°). *X. papuensis*° (fig. 92) has virtually no pleural arch (PL.A.(?)) and no doubt likewise leaps poorly. These thoraces have been described earlier in the section on Data and Observations, along with that of a bat-flea (*Nycteridopsylla eusarca*°) which also completely lacks the pleural arch, and it will be recalled, and can be seen, that there are some significant differences in the metathorax of the 4 depicted species which are inferior jumpers. However, these variations pale in comparison with those of 2 hystrichopsyllid nest-fleas, *Conorhinopsylla stanford*° (i.2) (fig. 85) and *Wenzella obscura*° Traub, 1953 (i.8) (fig. 86) which also lack the pleural arch. In the former species, an anomiopsylline, the pleural rod (PL.R.) is very thin and elongate, extending dorsad of the level of the third vinculum (VC.3), and here joins the dorsal margin of the metepisternum (MTS.) as the latter continues dorsocaudad, beyond what is generally the anterodorsal limit of the metepimere (MTM.). (The tanned portion of the dorsal margin of MTM. in this species disappears just anterior to the spiracle.) A semi-membranous region which is the vestigial lateral metanotal area (L.M.(?)) is represented as the vertical, narrow, dorsal section of MTS., near the apex of VC.3. The rhadinopsylline *Wenzella*° is obviously built on an utterly different plan, as witness the large, downward projecting triangle of the metanotum (fig. 86, MTN.) which fits between the metepisternum (MTS.) and the metepimere (MTM.). The metepisternum (MTS.) is reduced and terminates below the third vinculum (VC.3); it is overlapped by the large mesepimere (MPM.), and is caudally flanked by the pleural rod for its entire height. There is no sign of a lateral metanotal area, and even the squamulum is undeveloped. The mesepisternum (MPS.) is unusually straight and angled along the anteroventral corner, and the phragma of the nota (PH.2 and PH.3) exceptionally pronounced.

The variety of paths used to reach the same end emphasize the adaptive nature of the response. However, sometimes the final products, superficially similar in appearance, may be achieved for different reasons, as shown by Johnson (1957), who presented an informative and interesting discussion of modifications of the lateral metanotal area, citing and illustrating additional examples than those just mentioned. She made the significant point that although *Pulex* and allied forms, are good jumpers, the lateral metanotal area has ventrally merged with the metepisternum, a condition which is also seen in poor jumpers like *Anomiopsyllus*°, etc. Johnson explained the paradox by stating that in the former "the metathorax has become heightened and narrowed" and indicating that "consolidation of the metepisternum and the lateral metanotal area would lead to greater strength" (for facilitating leaping). Moreover, *Pulex*, etc. possess a pleural arch. "In *Anomiopsyllus*° and allies (nest fleas and poor jumpers), on the other hand, the pleural arch is missing and there are few strong internal sclerotized rods left which might serve to strengthen the metathorax so far as jumping is concerned."

There is at least one other thoracic feature besides the loss or reduction of the pleural arch and the lateral metanotal area, etc., that is often associated with the lessened ability to jump and the concomitant facility of crawling into cracks and crevices, i.e., the reduction or loss of the chitinized dorsal margin of the metanotal flange (or diminution of this "collar"), along with the loss of the metanotal spinelets. This is seen in many swallow-fleas, viz., those which occupy nests used perennially (and not just for one season) and which hence are not faced with the problem of seeking a new host elsewhere. The adaptive behaviour and physiological modifications of this first type of flea, which Darskaya (1959, 1964a) calls "settled" species, and of the "nomadic" fleas of the second category, will be discussed below (Section J). Here only the morphological features of the two types will be mentioned. In the "settled" group are the typical nest-fleas of the *C. arcuegens*° (fig. 90) and *C. delichoni*° pattern, which lack the pleural arch, but even those which retain the arch, are crawling, rather than jumping, species because the membranous or reduced metanotal flange permits a great deal of flexibility in the area of the junction of the thorax and abdomen, "while at the same time it deprives the flea's body of the fusion and compactness necessary for leaping" (Darskaya, 1959). Thus both *C. hirundinis* (Curtis, 1826), in which the metanotal flange is of this type, while the pleural arch is small and nearly contiguous with the top of the pleural rod, and *C. scopulorum* Holland, 1952, which has a fairly well developed pleural arch and a metanotal flange that is only somewhat modified, are adapted to crawl into crevices in the nest. In the typical nest-fleas particularly, but also in fleas like *C. hirundinis* etc., the caudal margins of the abdominal segments are more lightly tanned, permitting marked expansion of the abdomen when the flea engorges with blood prior to the long months of fasting when there is no bird in the nest, as is mentioned below. In contrast, fleas like *C. garei*, which have to leave their birthplace and seek out and/or leap on a host, have well developed pleural arches, "normal" metanota and are well tanned throughout.

Reduction of the posterior margin of the metanotum, including loss of apical spinelets occurs in some other bird-fleas, such as *Ornithophaga*, as noted by Holland and Loshbaugh (1958). This is presumably a flea of woodpecker-nests, or nests of tits, which also nest in tree-holes (Rosicky & Smit, 1965). The notable reduction in the number and girth of bristles; the narrow, feeble legs, the over-all light sclerotization, all suggest that the species of *Ornithophaga* are primarily "settled" or nest-fleas.

D. The Degree of Development of the Eye in Various Fleas

1. Comparative Size of the Eye. The degree of development of the eye of fleas varies tremendously amongst sundry groups of Siphonaptera, and sometimes even within a genus. Since some nest-fleas lack eyes, while in many they are reduced, and in some, are unusually large, it is necessary to discuss this topic before proceeding with subjects like the distribution of the nest-flea phenomenon in the Order.

It is well known that reduced or vestigial eyes occur in many unrelated fleas which parasitize subterranean or nocturnal hosts (Ioff, 1941; M. Rothschild & Clay, 1952; Traub, 1953; Traub & Barrera, 1966). Further, the allies of such modified fleas may have eyes that are much better developed, especially if they infest diurnal hosts. Amongst eyeless fleas of burrowing mammals are *Dactylopsylla* (iii.2) and *Foxella* Wagner, 1929 (iii.2), which infest Nearctic pocket gophers; *Pulex sinoculus* Traub, 1950 (ix.1), the only eyeless member of the genus and a parasite of Central American pocket gophers; (*Cryptoctenopsyllus*) *ingens* (i.4) a flea of the mole-like *Bathyergus*, which is essentially a blind and combless member of *Dinopsyllus* Jordan & Rothschild, 1913 (i.4) and hence its subgeneric status; and the monotypic *Cryptopsylla* (xi.2) which infests a South African bathyergid, (*Cryptomys*) with similar habits. Another such flea is the Angolan species for which C. Fox created the name *Rooseveltiella* in

1914, and which likewise parasitizes *Cryptomys*. Since this species is merely an eyeless *Xenopsylla* (ix.1), it is now called *X. georychi*. These hosts spend most of their life underground in dark burrows, and the eyes are minute in all of them. It is of interest that their fleas have followed a similar course of evolution. Although many species of *Ctenophthalmus* (i.3) have eyes that are only somewhat reduced, e.g. *C.* (*Ethioctenophthalmus*) *calceatus* Waterston, 1912, some species, such as *C.* (*Spalacoctenophthalmus*) *spalacis* Jordan & Rothschild, 1911, lack even a vestige. The latter is a flea of *Spalax*, a mole-rat whose eyes are so reduced that there isn't even an opening for the eye in the skin. The analogy continues with respect to hosts like moles (talpids) and burrowing voles (*Hyperacrius*), which spend much of their time underground—their fleas have greatly reduced eyes, as in the examples cited and illustrated by Traub & Evans (1967) and in *Hystrichopsylla talpae* (Curtis, 1826) (i.1), while burrow-frequenting or noctural animals like shrew-moles and shrews have small eyes, and again the condition is paralleled by their fleas, e.g. *Palaeopsylla* Wagner, 1903 (i.3), *Corrodopsylla* Wagner, 1929 (i.5) and *Doratopsylla* Jordan & Rothschild, 1912 (i.5), etc., in which the eyes are quite reduced. Nest-fleas of mammals which inhabit underground or enclosed nests (in hollow trees, etc.) and hence are in the dark virtually all the time, tend to have reduced or even vestigial eyes (figs 85, 86 and 92). Further, there is a direct correlation between the relative size of the eye of the flea and the amount of time the flea of underground nests spends on the host, away from its regular habitat. Thus, the less specialized neopsylline nest-fleas like *Epitedia* are not infrequently collected on the body of the rodent away from home, and in these fleas the eye is somewhat less reduced (fig. 98) than in the true nest-fleas (e.g. figs 85, 86, 92).

Mammal nests made of leaves and perched high in a tree probably admit more light than an underground one, but at any rate, squirrel-fleas like *Syngenopsyllus*° inhabiting such nests have eyes resembling those of flying-squirrels (fig. 97), i.e. somewhat smaller than those of diurnal fur-fleas like *Macrostylophora* (as in fig. 96) (which may live on diurnal squirrels residing in the same tree, or even the same nest, as *Syngenopsyllus*°).

Amongst nocturnal mammals with fleas with poorly developed eyes are bats in general; the New Guinean murines and marsupials infested with many genera of pygiopsyllids; rats in the Pacific Islands with *Sigmactenus* Traub, 1950 (iv.1) and *Neopsylla* (i.7), microtines with *Ctenophthalmus* (i.3) or *Amphipsylla* (iv.2), etc. However, some nocturnal or crepuscular animals have greatly enlarged eyes which enable them to utilize what little light may be available, e.g. lemurs, lorises, jerboas (*Allactaga*), flying-squirrels, etc. and it is of interest that a few fleas have developed along parallel lines, e.g. jerboa- fleas like *Mesopsylla* Dampf, 1910 (iv.2) and cricetid fleas like some *Ophthalmopsylla* Wagner & Ioff, 1926 (iv.2) (fig. 95), while some desert-*Xenopsylla* also have unusually large eyes (but others in the same habitat have very small ones) (Ioff, 1929; Traub, 1953). Mammals like flying-squirrels and dormice which are crepuscular or fairly nocturnal, and some species of rats with similar habits, have fleas with eyes that are well formed but small and oval (fig. 97). In contrast, fleas of diurnal mammals, such as squirrels, gophers, marmots, some carnivores, pigs, etc. (except in the case of fleas specialized for living in underground or dark nests), have very large and well developed eyes (fig. 96).

It should be noted that virtually all known bird-fleas (other than the sticktight fleas, which have followed another evolutionary path) have relatively well developed eyes, whether specific nest-forms like *Ceratophyllus arcuegens*° (ii.1) (fig. 90) or a good jumper like *C. styx* (fig. 91). In fact, the eyes of fleas of terrestrial birds (whether ceratophyllids, leptopsyllids or pygiopsyllids) are generally characteristically larger than those of mammal-fleas, even if closely related. (This is one of the intriguing parallels that have accompanied this convergence to the bird-flea habitus, along with presence of many long and fine setae, etc.) All of these bird-fleas parasitize diurnal birds, however, and since the fur-fleas of diurnal mammals have well developed eyes, in contrast to the crepuscular and nocturnal forms, it is not surprising that the eye of the active types of bird-fleas is large. It is unfortunate that there does not seem to be any specific flea of a nocturnal bird, because it would be instructive to examine its eyes. However, the tendency for relative reduction of the once-hypertrophied eye does exist in nest-forms amongst bird-fleas. In *C. delichoni*°, the eye is rather small, symptomatic of "inhabitants of an ill-lit nest cavity" (Darskaya, 1959). The trend is also exhibited by some fleas of sea-birds which nest in burrows amongst rocks on the ground of small islands, and hence where the fleas presumably spend much time in the dark. For example, in *Actenopsylla suavis* (ix.1) the eye is quite small (fig. 99), more so than in related pulicids of terrestrial, diurnal mammals. The host of *Notiopsylla kerguelensis* (ii.1) also nests in such burrows, in the subantarctic (Smit, 1957), although the fleas also occur on the bodies of the birds, and it is worthy of note that the eye of this species is conspicuously smaller and more irregular than that of *Hoogstraalia* Traub, 1950, another pygiopsyllid, but one which infests the bodies of diurnal birds.

2. VISION IN FLEAS. It is obvious, then, that the size and degree of development of the eye in the fleas is associated with the amount of light in the environment in which the flea evolved. The corollary would seem to be that the ability of the eye to function is equally correlated with this light-factor. Thus, it would be expected that squirrel- and bird-fleas could "see" better than vole- or mole-fleas, but there seems to be little experimental data in this regard. Rothschild & Clay (1952) state that the eyes of fleas "are in fact displaced dorsal ocelli. These relatively simple organs probably do little more than enable their owners to perceive the difference between light and darkness and thus would only assist them in finding a host if it were in their immediate vicinity." Bates (1962) reported that sand-martin fleas (which have a well developed pleural arch) clustered about a burrow-opening on a cliff could hop onto a bird hovering by the aperture for just a few seconds. However, the stimuli causing this reaction are not known, nor has it been determined if the excited fleas merely leaped at random and just a few were successful in alighting on the bird.

Bates showed that these martin-fleas, over-wintering as adults in pupal cases inside old burrows occupied the previous year, emerged in the spring and moved towards the opening of the burrow and there remained motionless, in clusters, with the heads pointing towards the aperture. It seems likely that the movement towards the opening, where the fleas would be in a position to leap onto a returning migrant that hovered by the hole, is a response to light, but this is not definitely known. However, these fleas were also shown to possess the ability to disperse from old burrows and emigrate as much as 33 meters and enter new burrows. While entrances to new burrows apparently were not detected by vision, the means to do so could not be determined, although it was learned that the fleas somehow recognize horizontal floors of burrows (as distinguished from the flat top of the bank) and tend to congregate there.

M. Rothschild (1969) reported that many fleas are negatively phototropic and jump away from a bright source of light (and the ones that she mentioned have relatively well developed eyes). Such fleas would generally move towards the shade, if given a choice between light intensities, but a few individuals would move *towards* the light.

Humphries has rendered a great service studying in detail such long neglected subjects as the behaviour of fleas, and among his important contributions are observations on *Ceratophyllus gallinae* (Schrank, 1803), the hen-flea (1968). Humphries noted that *C. gallinae*, after emerging as adults in the nest, are generally negatively phototropic for about 2 days, and as a result, stay in the nest rather than dispersing before mating. (The nests usually remain deserted by the hosts unless they return within that period.) Thereafter, the fleas exhibit a positive phototaxis and negative geotaxis, leave the nest and move upwards on the tree harbouring the nest. During the ascent, the fleas frequently pause for long periods and then resume climbing upwards if a host is not encountered. When in the immobile phase which Humphries termed a "stance", the fleas would immediately leap towards a small object that suddenly reduced the intensity of light. Humphries concluded that these responses were connected with locating a host and showed that fleas would readily leap upon an object the size of a small bird which moved about and paused on the branches. If, upon leaping, the *C. gallinae* missed Humphries' imitation-bird, they would alight on the ground and then climb up on the vegetation and start anew. As a result, even if they were only on grass, they would be in a position to leap upon a ground-bird casting a shadow.

Thus, while we really do not yet know how well fleas can see, it is apparent that they do respond to light and that those with eyes tend at times to move definitely or precipitously towards shadows. It therefore seems that regardless of other existing stimuli (vibrations, odor, carbon-dioxide, etc.), the sudden appearance of a host by the nest or by the burrow-aperture would cause a distinct change in light-intensity that would attract or spur fleas to leap upon their hosts. Contrariwise, such a shadow could not be thrown in a dark burrow underground, where the fleas lack the eyes to appreciate such changes anyhow. Darskaya (1954a) noted that *Citellophilus tesquorum* (iii.1) (which has well developed eyes) often cluster in great numbers about the burrow-opening of the suslik, *Citellus dauricus* (which is active during the day) and readily infest any ground-squirrel that puts its head in the hole or lingers nearby.

The facts that fur-fleas of diurnal, large mammals have well developed eyes, e.g. *Pulex* Linnaeus, 1758 (ix.1), *Ctenocephalides* (ix.1), *Pariodontis* Jordan & Rothschild, 1908 (ix.1), *Paraceras* (iii.1), *Oropsylla* Wagner & Ioff, 1926 (iii.1), *Thrassis*

Jordan, 1933 (iii.1), *Opisocrostis* Jordan, 1933 (iii.1), sundry vermipsyllids (x), infesting man, pigs, some carnivores, Old World porcupines, badgers, marmots, or prairie dogs, etc., and that these all seem to be excellent jumpers, lead me to believe that the large eye is of use to these fleas in finding their hosts.

The fleas of the small rodents which are diurnal, likewise have well developed eyes (unless, of course, they are nest-forms) and the same line of reasoning applies regarding the function of such eyes is further supported by Darskaya's detailed and well executed studies on *X. gerbilli caspica* and its desert-host, the gerbilline *Rhombomys* (1955). She states the "daily activity of these fleas is to a certain degree tied to the regime of light and daily activities of their hosts." It is of interest that Darskaya reported that *X. g. caspica* (which has a fairly well developed eye) will cluster at the mouth of the *Rhombomys* burrows, particularly if they had hatched out in a burrow-system that was no longer occupied (1955). Such hungry fleas have been known to instantly attack virtually any mammal near the opening and have been noted to follow such prospective prey for at least 2·5 meters. If they fail in their efforts to alight on the animal, they attempt to return to the burrow-openings.

The association between the size of the eye of the flea and the degree of development and utilization of vision in the host is so profound, that I was long disturbed over the eyeless condition in *X. papuensis*°, for I know of no truly burrowing mammals in New Guinea, and existing records were from *Pogonomys*, a somewhat scansorial rat. However, after collecting some of these fleas in *underground* nests of *Pogonomys* on several occasions, it became clear that this species was merely exhibiting the same trend noted in other nest-fleas elsewhere, even to the extreme reduction of the pleural arch.

In general, fleas possessing a *genal* ctenidium have a reduced eye, and the few exceptions are clearly adaptive. Thus, *Hoogstraalia* (ii.1) has a well developed genal comb and a large eye but it is a bird-flea, and as we have seen, an eye of that type is characteristic of such fleas. *Ctenocephalides* (ix.1) is similarly adorned, and since these fleas may hatch out anywhere in the haunts of the host, as indicated below, they may have to seek out and infest their hosts (large mammals) during daylight. As originally noted by Karl Jordan (1950) and discussed by Traub (1969), in fleas in which there is an evolutionary trend towards assumption of a vertical comb on the head, the vestigial eye is progressively displaced dorsad as the number of spines in the comb increases (e.g. *Peromyscopsylla*, *Leptopsylla* Jordan & Rothschild, 1911, *Sigmactenus*, etc.), indicating that the head-ctenidium in most cases is genal in nature (unlike the in helmet-fleas and in *Smitella* Traub, 1968 (ii.1)).

3. THE TYPES OF THORAX IN FLEAS WITH REDUCED EYES. Inasmuch as many characteristic fleas of bird-nests have well developed eyes but lack the pleural arch, while many mammal-nest fleas with such a thorax have very small or vestigial eyes, it is clear that reduction of the eye has proceeded independently of loss of the pleural arch, the former associated with the amount of light in the environment, the latter with lessening of the ability to jump. The two phenomena often coincide because conditions under which the environment is invariably in darkness are frequently those in which reduction in jumping-ability is also a useful attribute. Examples

have been cited in which the eye is large but the pleural arch is missing (e.g. many bird-fleas and nest-fleas of diurnal arboreal squirrels). In many species besides true nest-fleas the eye is so reduced as to be indistinct, and this topic merits consideration with respect to (1) species in which the pleural arch is present, and (2) species lacking the pleural arch but simultaneously showing adaptations for remaining on the fur of the host. In the first category are fleas of mammals like shrews, voles and other hosts that are primarily nocturnal and/or spend much time in burrows, but in which the fleas are adapted for attachment to pelage by means of combs of spines, dense or plural rows of bristles, or false combs of modified bristles. Examples like *Doratopsylla* (i.5) have already been cited. Here also belong other hystrichopsyllids such as *Neopsylla* (i.7), *Rothschildiana* (i.7), *Stenoponia* Jordan & Rothschild, 1911 (i.9), *Hystrichopsylla* Taschenberg, 1880 (i.1), etc., as well as leptopsyllids like *Peromyscopsylla* (iv.1), *Acropsylla* Rothschild, 1911 (iv.2), *Paractenopsyllus* Wagner, 1938 (iv.1), etc. and many chimaeropsyllids (xi.). It is noteworthy that eyes of this type are apparently unreported in ceratophyllids, although the more "degenerate" condition of virtual total absence occurs in the pocket-gopher fleas, which are members of this family. The condition of a reduced eye is approached, however, in *Malaraeus* Jordan, 1933 (iii.1) which is the name ascribed to a polyphyletic and somewhat anomalous assemblage of fleas characterized by the common character of a small but oval eye. Certain *Jellisonia* (iii.1) and *Kohlsia* (iii.1) also have an eye of this type. Very few pygiopsyllids have a well developed eye, but in most species the eye is fairly large and well pigmented, although ventrally excised. In the South American and Central American genus *Ctenidiosomus* Jordan, 1931 (ii.1), however, the eye is reduced and fragmentary, and the species have multiple combs of spines. In the second group, "blind" fleas which lack the pleural arch but which bear special or well developed pronotal or even genal combs, or are otherwise modified for host-attachment, are the insectivore-fleas like *Corypsylla* discussed in Section IV. C.2 above.

E. The Evolution of the Characteristic Pronotal Comb Ascribed to most Nest-Fleas

It has been shown above that throughout the Order, a variety of fleas have developed the habit of feeding on their hosts while the latter are in the nests, and have become modified accordingly. A wide assortment of hosts are involved, and their habits have affected the path of development of the adaptive responses of the fleas, as host and parasite evolved together in close association. As we have seen, the pronotal comb of nest-fleas infesting aerial hosts (bats and birds) (figs 89, 18, 90, 91) or those that parasitize arboreal, nocturnal hosts (figs 47, 88) tend to have an unusually large number of spines in the pronotal comb, as compared to allied taxa (figs 17, 46). However, nest-fleas of hosts nesting below ground or at, or near, the surface, tend to have pronotal combs in which there are fewer spines than "normal" and the spines are frequently short and broad (figs 67–84), and as previously indicated, such convergence cannot be ascribed to parallel proclivities in pelage. Instead, it seems that the pattern of the pronotal comb exhibited by fleas of this last category can only represent evolutionary stages in the general reduction of spines and bristles so characteristic of these nest-fleas, and which accompany such "modifications by reduction or loss" as has been noted for the eye, pleural arch, metanotum, size of metepimere, girth of legs, etc.

Examples have been cited above repeatedly showing how nest-fleas have lost or reduced these structures or a combination thereof, in approaching the configuration of the virtually nude species of *Anomiopsyllus*° and the combless, eyeless, slender *Wenzella*°. That reduction in the number of spines in the combs has accompanied the loss of bristles is not only indicated by the general trend, but by the fact that the genera with the fewest, and stoutest spines, e.g. *Megarthroglossus*° (i.2) (fig. 75) and *Conorhinopsylla*° (i.2) (figs 73, 86) are those with the most marked loss of setae. The setae seem to become narrower as they approach extinction in the course of evolution, but in the case of the pronotum the spines frequently become shorter and broader as in the nest-fleas. *Phalacropsylla* (i.7) approaches the last two genera with respect to the points mentioned. *Brachyctenonotus*° (iv.2) has a comb of extremely short spines, but these are fairly broad and the comb is almost full length (in height). *Calceopsylla*° (iv.2) duplicates the condition in *Brachyctenonotus*° regarding tiny spines, but the spines may be somewhat more slender and the comb is not quite as short. The pronotal ctenidium in many of these nest-fleas extends ventrad to near the vinculum, but it is definitely shortened in *Rhadinopsylla* (i.8) (fig. 72) and most neopsyllines (i.7) (figs 67, 70, 78, 76). In other instances, impending loss of the comb is indicated by the reduction in the vertical extent of the comb and in shortening of the spines, as in the chimaeropsyllids and in *Agastopsylla*° (i.3), or by loss of pigmentation accompanying reduction in length, as in *Mioctenopsylla* Rothschild, 1922 (iii.1) and *Brevictenidia* (iii.1), or as in both genal and pronotal combs in *Agastopsylla*. The loss of abdominal ctenidia by marked reduction of the number and size of the spines and by the shortening of the height of the comb as has been discussed by Traub & Evans (1967) and is also illustrated in the bat-flea *Nycteridopsylla eusarca* (v.1) (fig. 89).

A different mechanism for the loss of pronotal spines can be seen in *Corypsylla ornata*° (i.8) (which may not be a true nest-flea in that it is simultaneously adapted to remain on the host) and involves sexual dimorphism. Here the male has a full length comb of spines, of which the upper fourth are long and stiletto-like, and the emainder becoming progressively shorter and less acutely pointed. The shortening in length is accomplished mainly by the loss of the base of the spines, and not merely by abbreviation of the apices; the proximal ends of the spines forming a sigmoid line whose lower ⅔ is markedly convex. The original full length of the spines is indicated by pale outlines and caniculi. In the female, however, the dorsal ⅗ of the comb consists of stiletto-like spines, which also become progressively smaller, but the lower ⅖ of the comb is represented only by pale blunt nubbins of spines which are more like denticles, with long caniculi proceeding to the former base of the comb.

The two known genera of malacopsyllids (xiv) (both monotypic) are not nest-fleas, although they have followed another path leading toward reduction and loss of combs, namely the development of the "sticktight" habit. It is instructive that *Malacopsylla* Weyenbergh, 1881 has no ctenidia at all, but that in *Phthiropsylla* Wagner, 1939, the pronotal comb is represented by but 3 very short, broad spines or "teeth" which are widely spaced.

The tendency towards loss of ctenidia is general throughout nest-fleas in the Order, as shown by the fact that combless members amongst such fleas occur in 5 of the families which include nest-species, while the trend is also demonstrated in the sixth (Leptopsyllidae). There can be little doubt that intermediate steps in the evolutionary path, and not the structural peculiarity of the pelage, account for the convergence of patterns of pronotal combs seen in these nest-fleas inhabiting underground nests, etc.

F. Distribution of the Nest-Flea Phenomenon in Siphonaptera

Although nest-fleas occur throughout the Order, it is apparent from what has been written above, that the phenomenon is much more common in certain groups of fleas than in others, and that the degree of specialization exhibited varies considerably. Both of these points can presumably be explained by the following factors: (1) The duration and extent of the association between the fleas and their respective hosts. (2) The phylogeny of the fleas and of their hosts. (3) The ecology of the area concerned. (4) The habits of the host. (5) The habits of the fleas. The relative geological ages of the various groups of fleas and some of their hosts will be treated at some length in a subsequent article (Traub, in preparation) but a brief discussion of certain elements is warranted at this time, while considering the other points.

The vast majority of the nest-fleas are members of the Hystrichopsyllidae (referred to as family i), where representatives occur in 4 of the subfamilies. There were several examples cited for the Ceratophyllidae (iii), but relatively few for the Pulicidae (ix) and Leptopsyllidae (iv). The proportion of nest-fleas is fairly high in the Chimaeropsyllidae (xi) but the family is a small one and only a few species are actually involved. The condition is rare amongst known Pygiopsyllidae (ii) but the dearth may be more apparent than real, for the following reasons. (1) The family is primarily Australian–New Guinean in distribution, with relatively few species occurring in the Asiatic–Pacific islands, the Indo–Malayan region and Central Africa. Throughout much of their range therefore, the pygiopsyllids are found in regions of heavy rainfall and hence where mammals make few underground nests because of the high water-table and flooding, and where relatively dry, hollow cavities in logs, stumps and trees are rare or absent. In such an environment there has been little opportunity for development of the nest-habit in fleas, except perhaps for those infesting arboreal hosts living in tree-holes or making some sort of aerial nest that adequately sheds water. (2) Relatively few mammal-nests have been examined for fleas throughout the entire range of the pygiopsyllids, and even the fur-fleas of indigenous Australian rodents and marsupials are inadequately known. The same is true for body-fleas in the other areas, save New Guinea. It seems likely that pygiopsyllid nest-fleas await discovery, perhaps in xeric areas of Australia or in arboreal species elsewhere.

Very little has been written about the phylogeny of the various families and other groups of fleas (Traub, 1968), and it is beyond the scope of this article to do more than point out that the families Hystrichopsyllidae and Pygiopsyllidae are regarded by me as being ancient and primitive in many respects (but specialized in others), while the Pulicidae is considered to be a very old, but yet more advanced family than the first two, and the Leptopsyllidae, Ischnopsyllidae and Ceratophyllidae are deemed younger. Reasons for these views are cited in another article (Traub, in preparation), but are based on three considerations: (1) Morphology, including general skeletal structure and comparative anatomy of the aedeagus. (2) Host-relationships. In general, the more primitive and oldest fleas are associated with the more primitive hosts, and the more specialized fleas with the more advanced (and younger) mammals. (3) Zoogeography. Fleas essentially restricted to two or three of the southern continents are believed to have spread amongst those areas when island-hopping links still existed between them, well before Australia and South America became isolated.

In general, the hystrichopsyllids infest mainly insectivores, cricetids, and sciurids, while the ceratophyllids, on the whole, parasitize mainly cricetids and sciurids, and some murids. Relatively few hystichopsyllids (e.g. some *Neopsylla*) and ceratophyllids (e.g. certain *Nosopsyllus*) infest the genus *Rattus* and it is significant that there are no known nest-fleas specifically associated with *Rattus*, which is believed to be a recently evolved group. Leptopsyllids are rarely specific to insectivores except perhaps for tenrecids in Madagascar, and instead are found on murids and, particularly in the Old World, on cricetids. Some leptopsyllids are associated with dipodids and gerbillines and a few with ground-dwelling Palaearctic sciurids and lagomorphs. The pygiopsyllids are, on the whole, either fleas of marsupials or murids. Pulicids are found to parasitize a broad range of hosts when considered as a family, but some specialization is shown by certain of the subgroups. Many are sticktight fleas or "burrowing" species like *Tunga*, as has been indicated, and these need not be considered further. The spilopsyllines include rabbit-fleas which tend toward semi-sessile habits, and the two genera of nest-fleas of marine birds treated elsewhere. The xenopsyllines are primarily fleas of gerbillines (and hence occur in rather xeric areas) or are mane-fleas. The archurieopsyllines include carnivore-fleas like *Ctenocephalides*, hedgehog-fleas, and one odd rabbit-flea, a Madagascar tenrec-flea and the African *Aphropsylla*, whose true hosts are unknown.

The questions arise as to why the bulk of the nest-fleas occur in the hystrichopsyllids, why the phenomenon exists in so many subfamilies and tribes thereof (e.g. 7 of 8 Anomiopsyllinae genera and 8 of 11 genera of Neopsyllinae), and why the examples include some of the most highly specialized nest-fleas, e.g. *Anomiopsyllus*° and *Wenzella* . Inasmuch as the host-associations and morphology of the hystrichopsyllids suggest that the family is an ancient one, the obvious answer is that hystrichopsyllids and their hosts have been associated intimately for eons, long enough for the nest-habit of fleas to have evolved and progressed to the point of extreme specialization by reduction. Nevertheless, it must be pointed out that, for unknown reasons, very few instances of the relationship involve insectivores, which are believed to be low on the phylogenetic scale. Virtually the only examples are some species of *Rhadinopsylla*, and these are not highly specialized, and may not be specific. Perhaps if more were known about the fleas of nests and shrews in North America and northern South America, some such true nest-fleas would be discovered, but it may be that the nests of shrews are too transient for such fleas to have evolved, and this is why virtually all shrew- and mole-fleas are adapted for remaining on the host. Regardless, hystrichopsyllids are found on all continents, but have an extremely discontinuous distribution, e.g. huge gaps over most of South America, and known endemicity in a restricted portion of Australia, with the geographically closest members of the family occurring in Borneo and Indonesia. Such a range also bespeaks of antiquity, as does the existence of two endemic subfamilies in Africa. Nest-fleas occur in virtually all of these areas, perhaps also including Australia. The highly modified *Anomiopsyllus*° and *Wenzella*° are parasites of heteromyids, a group that arose in the early Oligocene, with some modern genera occurring at least in the Miocene (Simpson, 1945). A large proportion of these hystrichopsyllid nest-fleas (e.g. *Megarthroglossus*°, *Stenistomera*°, *Callistopsyllus*°, etc.) are (like *Anomiopsyllus*°) associated with the fauna of the deserts of North America, another phenomenon that was Oligocene in origin. For these reasons, the extreme age of the family and its associations seem to have been an important factor in the evolution of the nest-habit.

The sciurids and leporids, however, are older than the rodents mentioned above, and yet the family of fleas most closely connected with squirrels, the ceratophyllids, include only a few nest-fleas. Here we must differentiate between the geologic age of a group of mammals and the duration of the association of the fleas with such animals, for they may be very different. For example, although birds arose far back in geological time, their parasitism by fleas must be relatively recent, for the sundry bird-fleas, representing several different families, are all supposed to be derived from mammal-fleas (Rothschild & Clay, 1952; Holland, 1964; Traub & Barrera, 1966). That this was so, was well known to Jordan (1937) and N. C. Rothschild (1917), and Ioff (1928) also referred to this phenomenon in pointing out that bird-fleas of the *Ceratophyllus gallinae* group are related to mammal-fleas now referred to as *Monopsyllus*, e.g. *M. sciurorum* and *M. tamias* (Wagner, 1927). Ioff further noted the close affinities of the rodent-infesting *Frontopsylla* with those on birds (but which are today called *Orfrontia* Ioff, 1946). Moreover, the bird-infesting genus *Ceratophyllus* itself is believed to be of polyphyletic origin. Another point is that the particular genus, tribe or subfamily of host may be relatively recent in origin even though the stock is ancient. One feature that is quite striking is that there *are* quite a few nest-fleas parasitizing sciurids, but most of these not only are hystrichopsyllids, e.g. *Conorhinopsylla*°, *Megarthroglossus*°, *Rhadinopsylla*°, *Epitedia*, *Tamiophila*, etc., but genera which also includes species which are nest-fleas of peromyscines and other cricetids, and hence may represent recent transfers to sciurids. Actually, true squirrels are known from the Miocene, while the groups of tree-squirrels may be much younger, but the fossil record is scanty (Simpson, 1945). It may very well be the relative youth of the tree-squirrels that accounts for the comparatively small number of nest-fleas known amongst such hosts, and for the low degree of specialization shown by such ceratophyllids, despite the selective pressure exerted, for such an evolution, by the hazards of existence encountered by fleas in the high trees. It is noteworthy, however, that the bulk of the ceratophyllid nest-fleas of mammals is found amongst the parasites of squirrels nesting in high trees or amongst flying-squirrels. Another factor for the apparent dearth of nest-fleas in this family is the presumed modernity of ceratophyllids as compared to the hystrichopsyllids—there hasn't yet been time for the marked reduction in head, thorax, etc. to occur.

Offhand it seems strange that so few nest-fleas are known to parasitize the Marmotini, the tribe including the northern ground-squirrels (*Citellus*, etc.), marmots (*Marmota*), prairie-dogs (*Cynomys*), chipmunks (*Tamias*, etc.), and which is believed to have arisen in the Miocene (although all records save for *Citellus* are Pliocene or later). A wealth of genera and species of ceratophyllid fleas such as *Citellophilus* Wagner, 1934, *Callopsylla* Wagner, 1934, *Thrassis, Opisocrostis, Oropsylla, Diamanus* Jordan, 1933, are associated with these rodents that essentially are ground-squirrels but which vary in size from small to huge, but only the occasional species like *Callopsylla dolabris* (fig. 84) seem to be developing the nest-habit. (It should be noted that the fur-fleas of *Citellus* and other true ground-squirrels, such as *Citellophilus, Opisocrostis, Thrassis* and *Diamanus*, do not exhibit the tendency towards broadened subventral pronotal spines of the fleas of the arboreal and semi-arboreal squirrels.) The other nest-fleas occasionally encountered on chipmunks and *Citellus*, etc., are hystrichopsyllids, e.g.,*Tamiophila*, as has been pointed out to be the case for the nest-fleas of tree-squirrels. The marmotines burrow and nest underground in habitats that should favour the production of nest-fleas, for they abound with other types of fleas, some of which have long palpi (like *Diamanus*, etc.), indicating feeding at leisure. One contributory factor may be that these hosts are all diurnal, meaning that any flea which lingered on the host would be exposed to light considerably, especially if it fell off—or developed from an egg that had been hatched out on the ground surface. Fleas with reduced eyes would be at a selective disadvantage under such conditions, and it is reiterated that virtually all of the nest-fleas of mammals have hosts that are crepuscular or nocturnal.

Many, if not most, of the ceratophyllids of burrowing rodents are well known for swarming about the opening of the burrow (Darskaya, 1954a, 1955), and this habit no doubt is all associated with the presence of a well-developed eye. In this way, the fleas are able to leap upon rodents that approach or enter the burrow, or even pursue them for a while (Darskaya, 1955). In all probability, these fleas have hatched out in the nest or in various depths of the burrow and move toward the light source at the aperture, as Bates (1962) observed for the perambulatory type of sand-martin flea. Thus, the evolutionary trend of the ceratophyllids has in general been in directions opposed to the formation of true nest-fleas, although the time factor of length of association between host and flea may also be important.

Leptopsyllids on the whole have followed much of the route of the ceratophyllids insofar as concerns evolution of habits of infestation, but have detoured with respect to host-range and have become delayed regarding distance traveled. Thus, very few genera and species occur in North America (where all native forms except two are associated with lagomorphs), whereas the ceratophyllids are the dominant members of the Siphonapteran fauna in that part of the world. Leptopsyllids not only infest cricetids but to a great extent parasitize murines, one species having even accompanied *Rattus* to New Guinea, whereas there are no native murids in the New World. (The last-mentioned point no doubt helps account for the dearth of leptopsyllids in North America.) There has been little association of leptopsyllids with sciurids and virtually none with tree-squirrels in particular. Except for fleas of murines (which are nocturnal), nearly all leptopsyllids have fairly well developed eyes, while the bird-infesting species have large eyes. In general, they seem to be good jumpers and rodent-species may be common around burrow apertures, while nearly all are modified for remaining on the body of the host. The few known species that seem to be nest-forms have converged along the familiar lines indicated above. One relevant and possibly important factor in this discussion is that there still is a great deal to be learned about the nest-inhabitants of desert rodents throughout much of Asia (excluding well studied areas of the U.S.S.R.). The majority of North American nest-fleas are found in xeric areas, and very few leptopsyllids are represented in the fauna, whereas members of this family are common and wide-spread in the Asian counterpart terrain. The African nest-fleas are also inhabitants of deserts and semi-deserts, in the main. The equivalent fauna in Asia may therefore be better developed than current data indicate.

The answer to the question as to why nest-fleas are poorly represented amongst pulicids lies in the evolutionary sequences observed in that family, viz., development of sticktight fleas or else active species with well developed eyes, which are good jumpers and which are so highly adapted that they can feed and thrive on an exceptionally broad variety of hosts. It should be noted that just because a flea has sticktight habits, it does not mean that it is *ipso facto* a poor jumper, for the behaviour of a flea after it finds and attaches to its host may be quite different than it was beforehand. Some sticktight fleas like *Echidnophaga* Olliff, 1886 (ix.1), which are essentially sessile after attaching, are excellent jumpers. Thus, *E. gallinacea* (Westwood, 1875) can leap 200 times its own length (M. Rothschild, 1969), a fact that is useful when it encounters its usual prey of medium or large size, such as rabbits, carnivores, pigs, chickens, etc.

The catholicity of pulicids regarding hosts is illustrated by the so-called cat-flea *Ctenocephalides felis* (Bouché, 1835) which has not only been collected in numbers on all sorts of carnivores, including dogs, foxes, wolves, jackals, tigers, *Felis bengalensis* and other "wild cats," racoons, coati-mundi, weasels, mongoose and other civets like the binturong (*Arctictis binturong*), but on man, opposum, cattle, horses, sundry rodents, lagomorphs, hedgehogs, bats and the armadillo, etc. (Traub, 1950; Hopkins & Rothschild, 1953; Hoogstraal & Traub, 1963a, b, 1966; and unpublished data). It has also been known to feed on lizards (Fox, Fox & Bayona, 1966) and the related *C. canis* (Curtis, 1826) has been reported sucking blood from a lizard (Jäth, 1952). There are not many records of *C. felis* from rodents, as compared to the large mammals, but this, I believe, reflects its superior ability as a jumper, and not to any inherent predilection or aversion, since it ordinarily vaults too high to strike a rat-sized animal. The plague flea, *X. cheopis* is notorious for feeding on man as well as rats, but has a very broad host-range in general, from a variety of murines and other rodents, to shrews, lagomorphs and bats, as cited by the sources mentioned above. In this case, the vast majority of records are from small hosts, for *X. cheopis* does not leap as high as *Ctenocephalides*. *X. gerbilli caspica* has been reported to feed on lizards (Darskaya & Besedina, 1961; Kulakova, 1964).

The majority of the pulicids are compact, i.e. relatively short and broad, a type of build that is often seen in fleas that are good jumpers. The species, whose life-histories are known, tend to lay eggs loosely among the hairs of the host, as in *Cteno-*

cephalides, so that the larvae and adults are apt to emerge in the haunts of the host, rather than in the nest. Larvae of the desert-species *X. conformis* (Wagner, 1903) have been found to be abundant in the rodent-burrow, at the entrance, indicating that the eggs can develop wherever they fall, if conditions are favourable (Darskaya et al., 1962). In the case of large mammals (e.g. *Pulex* and pigs) this can be almost anywhere. This particular trait of egg-laying is associated with fleas with large eyes and a well developed pleural arch, as has been noted. For these reasons, development of the nest-habit in the Pulicidae has occurred only under special circumstances, as in some of the fleas associated with burrows of marine birds and in underground nests of *Pogonomys*, etc. A few *Xenopsylla* associated with the desert have small eyes, as befitting ectoparasites of nocturnal hosts that wouldn't emerge from their burrows during the heat of the day.

The evolution of the nest-habit virtually by definition is limited to fleas of hosts that (1) have a specific nest or burrow and (2) reside there continuously or else return to live or breed there the following year or season. It is probably for this reason that no true nest-fleas are known amongst the rabbits and hares (leporids), and that instead, the rabbit-fleas often act somewhat like sticktight species. It is noteworthy that the rabbit-warrens often do swarm with fleas when the young rabbits are born, but this is presumably due to transfer of fleas from the adult rabbits, as part of the synchronization of the fleas with the hormones of the host, as has been clearly shown for the European rabbit-flea (M. Rothschild, 1965a, b). The splendid fleas of the Mexican volcano-rabbit, *Romerolagus* described by Barrera in 1967, defied discovery, despite intensive search of adult *Romerolagus* over a period of years, until the nestlings were located and examined.

G. The Association Between the Mode of Egg-Laying and the Nest-Flea Habit

Intimately associated with the pattern of behaviour exhibited by various kinds of fleas in locating a host, is the factor of the particular site where the flea-larvae transform into pupae and hence where the adults emerge. In this regard it is important to note that not all fleas deposit their eggs loosely amongst the hairs of the host as in the case of the cat- and dog-fleas (*Ctenocephalides*) (ix.1) so that the eggs may drop off anywhere in the haunts of the host. Some fleas, such as *Orchopeas howardi* (Baker, 1895) (iii.1) leave the host and glue the eggs to bits of debris in the nest and then return to the mammal. In the latter case, the immature stages are to be found in the nest, and that is where the newly emerged adults are to be found. This is why some species of fleas are common in the nests, especially at certain times of the year, even though they are not true nest-fleas in the sense we are using the term. I believe that *Stenoponia* and *Hystrichopsylla* are fleas that lay their eggs in the nest and hence are in this category, but real data are lacking. *Stenoponia* females are often noted with two huge eggs in the abdomen (as so beautifully depicted in a colour photograph by Sakaguti, 1962), in contrast to ceratophyllids, which may have 8–12 smaller, but fully developed ones. It would be surprising if *Stenoponia* could spew out such huge eggs while on the fur of an active host. Moreover, *Stenoponia* is a winter-flea, according to our observations in Pakistan and as indicated by available and published records in the U.S.A. and Mexico, and adults are collected only during the cold season. The larvae apparently take nearly a year to develop, and the unmistakably large larvae can be seen in the rodent-nests in the summer, if not earlier. All these points suggest that the *Stenoponia* larvae could not find suitable conditions just anywhere, and that, instead, the life-cycle has become attuned for nest-development. In my view, this is also the case for other fleas which are frequently found in nests but which are modified along the lines of a fur-flea (and which Ioff (1929, 1941) has referred to as "nest fleas," along with the specialized fleas for which we used the term).

Vaschenok (1967), in fine detailed studies on the ecology and life-history of the pulicid *Echidnophaga oschanini* Wagner, 1930, has provided relevant observations along these lines, which also emphasize the physiological attunement of the flea to its host. This species lays its eggs only when in darkness, and since its host (*Ochotona*) is diurnal, the result is that the eggs are deposited only when the pika is in its burrow. Further, since the eggs are dry and non-adhesive, they immediately fall to the floor of the nest or lair, where there is an environment suitable for development of the larvae.

It is also clear that the egg-laying habits of the squirrel-infesting *Orchopeas*, mentioned above, are also adaptive, for adults emerging in the nest are ensured of food, especially during the breeding season, whereas larvae developing from eggs dropped indiscriminately from the fur of an active arboreal host may have a difficult time finding a suitable environment for development, as might the newly emerged adult flea in locating a squirrel. Thus it would seem that just as there are nest-fleas, so there may be nest-larvae, although so little is yet known about the larvae of most kinds of fleas that it is premature to discuss possible morphological or physiological differences between the free-living larvae and the nest-bound ones. The possible significance of the specific requirements for a nest environment for some species has been indicated in the first paper of this series (Traub, 1972a) when it was pointed out that the species of *Medwayella* infesting ground-squirrels had never (or extremely rarely) been collected on arboreal squirrels, and it is believed that the conditions in the nest account for these differences.

H. Reduction of Combs, etc. in Fleas other than Nest-Fleas

Inasmuch as the absence of combs and reduction in chaetotaxy is characteristic of many nest-fleas, it is desirable to refer to 3 families in which all members bear these features but are not nest-fleas in the ordinary sense, viz., the Vermipsyllidae (x), Coptopsyllidae (xiii) and Malacopsyllidae (xiv). The majority of species of Vermipsyllidae belong to the genus *Chaetopsylla* Kohaut, 1903, and all of which are parasites of carnivores, and are characterized by the following: large eyes; frequently fairly short mouthparts (but at times they are quite long, reaching the fore-trochanters); a well developed pleural arch and leathery, flexible abdominal segments, permitting great expansion. This unusual combination of characters can be explained by their habits—they are primarily den-fleas, specialized to feed for long periods on hibernating hosts during the winter months and early spring and/or when the young carnivores are born in the den. Presumably the eggs are laid loose among the fur of the host (as in the case of the vermipsyllids mentioned below) and hence can fall off at any time and develop into larvae wherever the micro-environment is suitable, although many of these will be in the den. Many of the carnivores are diurnal, but the large eyes of the flea no doubt are also useful in enabling the newly hatched fleas to find their host, particularly if out-of-doors. As is to be expected, in the case of fleas infesting large mammals, especially if prone to hatch out on the ground, the vermipsyllids are good jumpers when unfed. Virtually all the records are from the cold parts of the year, or else are from alpine or subarctic heights in the mountains, indicating the species spend the rest of the year as eggs, larvae or pupae. The dense fur of the hosts enable these large fleas to hide easily if on the body, and to crawl with dispatch when grossly engorged.

The other two genera of vermipsyllids, *Vermipsylla* Schimkewitsch, 1885 and *Dorcadia* Ioff, 1946 are extreme in their adaptations for existence as "alakurts", grub-like fleas infesting the dense wool or thick patches of hair on the bodies of various ungulates in the high mountains of Central Asia. Very few fleas parasitize ungulates, probably because such hosts do not have dens or nests where the larvae have a good chance to develop, and the fleas an opportunity for a steady diet. Moreover, the hosts of the alakurt frequent forbidding terrain, and all in all, very few other kinds of fleas could possibly complete their life-cycles under such conditions. However, the alakurts emerge in the alpine fields and bogs at the onset of cold weather, when the horses, sheep, deer, etc. have dense coats, and the fleas, which have large eyes and are excellent jumpers, actively seek and leap upon their prey in daylight. (At night it is too cold for the fleas to move about, even if they were able to locate their hosts.) Their success, at least in the case of domesticated animals, is indicated by Ioff's report (1950) of 7000 specimens on a single sheep. In *D. dorcadia* (Rothschild, 1912), the size of the newly emerged female is stated to increase more than 250-fold as it engorges on its host and as the eggs mature (Ioff, 1950). The males remain active on the host and do not feed much, but the females remain *in situ* on the host for very long periods (as expected in fleas with such long mouthparts). Grossly-swollen females can crawl maggot-like, or by a wiggle induced by peristalsis-like waves, since they are too fat to use their legs. *Dorcadia* have been observed to remain on a single host for 3 months although moving about from time to time. The eggs are deposited loosely amongst the hairs or wool, and eventually fall to the ground, where the eggs may remain viable but unchanged all winter. The larvae emerge in the spring, feed on organic debris, often in clumps of dried sod, and pupate in the late summer or fall. It is of interest that these larvae, which may hatch out in the open, are believed to have a rudiment of an eye (Ioff, 1950) unlike other known flea-larvae, which are generally in the dark.

It is important to note that the Vermipsyllidae are believed to have always been without combs of spines (at least on the pronotum), unlike the families of fleas we have been discussing heretofore (Jordan, 1947; Holland, 1949; Traub & Evans, 1967),[10] and thus only superficially resemble the nest-fleas which have lost the combs by reduction. As can be seen from the above outline, the vermipsyllids differ likewise in other details of structure, habits and hosts—one notable development is the labial palpus of 25 joints in *Dorcadia*, instead of the 5 segments seen in most fleas.

The Coptopsyllidae are another family that may have lacked combed ancestors since none of the species possess even apical spinelets on the abdomen, and there is no trace of genal or pronotal combs. One species even lacks the mesonotal pseusosetae which is supposed to represent a rudimentary (incipient) ctenidium—a condition that is rare in most families of the Order. Here again the low number of abdominal bristles and the presence of very long mouthparts are suggestive of nest-fleas, but the large eye and frequent presence of extremely long tibial bristles, and the supernumerary plantar tarsal bristles are not. Moreover, the abdominal bristles are often long. The marked length of the tibial bristles is suggestive of other desert-fleas, e.g. some *Xenopsylla*, where Ioff (1941) believed they were used in burrowing into the sand to enable the flea to escape the sun and heat. The pleural arch is large and hence although the lateral metanotal area is higher than long, I believe they may be fair jumpers. As Lewis (1964) points out, a fairly large number of species have been described, but only a few specimens have ever been collected, in most instances. Too little seems to be known about their habits to warrent further discussion.

The Malacopsyllidae (xiv) include 2 South American monotypic genera, *Malacopsylla* and *Phthiropsylla.* These, although combless or essentially so, and with reduced vestiture are obviously modified as "sticktight" fleas, i.e. to stay attached to the host for long periods and feed until swollen with blood (hence the specific name *M. grossiventris* proposed by Weyenbergh, 1879). Thus, the cuticle is leathery and bears longitudinal pleats, permitting great expansion, while the tibial bristles are extremely short and stout, as are some of the tarsal bristles, and even the plantar bristles are stout or even subspiniform. The eye is large and the pleural arch well developed, indicating these fleas seek out their prey, leap upon them and catch and hold on by means of the specialized tibiae and tarsi, and therefore are not nest-fleas. These conclusions are the same as those reached by Johnson (1957). The sticktight habit recalls the case in the Pulicidae (ix), where the hectopsyllines and many of the Pulicinae are combless, have large eyes, are excellent jumpers and are fixed or semisessile on the host (but which stay attached by means of anchoring mouthparts).

I. The Possible Relation Between the Pronotal Comb and a Frigid Environment

Smit & Dunnet (1962) in remarking on the facts that in the Antarctic *Glaciopsyllus antarcticus*°, the pronotal comb is represented only by pseudosetae (or by apical spinelets), and in the Arctic *Mioctenopsylla* is greatly reduced (i.e. the spines are extremely small and pale), stated that "there may conceivably be a partial correla-

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[10] It is not clear as to whether Jordan (1947) meant that the vermipsyllids never had any combs on any of the segments or if he had only the pronotum in mind. Combed fleas always seem to have at least the pronotal comb, and Jordan believed that the pseudosetae represent incipient combs. It would therefore seem that the presence of pseudosetae on the pronotum, which is the case in vermipsyllids, rules out the possibility that the ancestor of that flea had a pronotal comb, and it would then follow that the ancestral flea lacked other combs as well. This may very well be the case, but the Antactic flea *Glaciopsyllus antarcticus*° is unique in the family Ceratophyllidae. in lacking a pronotal comb, and presumably has pronotal pseudosetae, yet apparently all students of Siphonaptera believe it is descended from combed fleas. However, the prothorax seem to bear seta-like apical spinelets as well (Traub & Evans, 1967), and the relationship between these and true pseudosetae, or the structure resembling pseudosetae in this species, requires further study. If there are no true psuedosetae on the pronotum and the spinelets represent vestigial spines, Jordon may be correct.

tion between temperature and development of ctenidia". This is an interesting possibility and more information is needed before it can be evaluated. However, data at hand lead me to question it. None of the fleas collected by us in Arctic terrain at 12000 ft elevation in the Himalayas of West Pakistan, where the ground is frozen 9 months of the year and where it may snow in summers (Traub & Evans, 1967), showed any such tendency. Thus, in species like *Ctenophthalmus golovi* Ioff & Tiflov, 1930 (i.3) and *Frontopsylla elata* (Jordan & Rothschild, 1915) (iv.2), the combs are similar to allied forms, instead of being reduced, although it is true that these species are also found in less frigid climes and hence may not be valid examples. However, *Monopsyllus thambus* (Jordan, 1929) (iii.1) is a flea of the far north and of subartic heights in the Rocky Mountains, and it can be seen by comparing fig. 57 with that of fig. 59 (*M. wagneri*, another *Peromyscus*-flea, but a temperate one), that there is no reduction in the comb. Alaskan and other northern fleas show no loss regarding number or size of spines unless they are nest-fleas.

Perhaps there is more reason to believe that the reduction of the comb seen in *Mioctenopsylla* and *Glaciopsyllus*° Smit & Dunnet, 1962 is correlated with the fact that other fleas of sea-birds lack combs, viz. *Notiopsylla* (ii.1), *Actenopsylla* (ix.1), *Ornithopsylla* (ix.1), 3 species of *Xenopsylla* (ix.1) and *Parapsyllus* Enderlein, 1903 (iv.2).[11] Further, *Notiopsylla* is highly exceptional amongst pygiopsyllids in not bearing ctenidia, while *Actenopsylla* and *Ornithopsylla*, spillopsyllines, are the only members of their subfamily with this trait. However, no *Xenopsylla* bear combs and no rhopalopsyllid (to which family *Parapsyllus* belongs) has a true ctenidium either. As indicated above, I believe the reduction of the comb seen in these bird-fleas is associated with their being primarily nest-fleas.

J. STRUCTURAL AND BEHAVIOURAL VARIETY WITHIN A UNIFORM ORDER OF INSECTS

The Order Siphonaptera is so distinctive and basically uniform that Snodgrass (1946) pointed out that even any small piece of the exoskeleton of a flea can be promptly recognized without question. Yet, within this overall plan, believed to be of undoubted monophyletic origin (Jordan, 1947), much more diversity exists in behaviour and structure than is generally appreciated. There are the hypodermal Tunginae like *Tunga*, which are so specialized that the tiny females penetrate into the superficial layers of the skin of the host and ultimately lie almost completely within a cyst, with just the apex of the abdomen protruding. Here the flea may remain for weeks, engorging on blood repeatedly, and as the abdomen fills with dozens of eggs, the females may reach the size of a pea, extruding eggs to the outside world intermittently. The sticktight fleas (other Tunginae and the pulicine *Echidnophaga*) act in a somewhat similar way but remain external, anchored by long serrate mouthparts. In both groups combs of spines are absent, and the vestiture reduced in general; the thorax is extremely narrow and telescoped; the head very large and angulate, so that it may be pressed against the host as the flea attaches; while the abdomen is capable of marked extension.

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[11] *Parapsyllus* is a member of the Rhopalopsyllidae, all of which lack true combs, and hence the absence of a comb in this genus may have nothing to do with the parasitism of sea-birds. On the whole, the family infests rodents and is essentially Neotropical, but one other genus may also be associated with sea-birds, namely the Argentinian *Listronius* Jordan, 1942, which includes 3 species all of which are known only from 1 or 2 specimens. One of these species, *L. robertsianus* (Jordan, 1939), has been found only in the Falkland Islands, on two occasions, once in the burrow of sea-birds and once on an ornithologist.

Others like the pulicine rabbit-fleas are sessile only for certain periods and move about occasionally to a new site or to move onto the young of the host. The vermipsyllids and malacopsyllids, like the tungines, have a leathery integument and hence are capable of gross enlargement, but they are external ectoparasites and not as fixed. Other attributes of these fleas have already been mentioned. Many kinds of fleas are active on the host, and move about and feed frequently, like the familiar cat-fleas. These are fur-fleas, and possess combs of spines and rows of stiff backward projecting bristles to enable them to remain safely on the host. Variants on this theme, occurring throughout the Order, possess spiniforms or other modified types of bristles along or near the front margin of the head so that they can hook onto hairs while feeding or resting (Traub, 1968). Such "thorny-headed" fleas are further adapted in having the head flattened and in possessing stout procoxae, modifications which enable them to appress their heads against the body of the host while hooked onto the bases of hairs (Traub, 1968, 1969). Most of the above types of fleas have a well developed pleural arch and are good jumpers, enabling them to, at least, find a host before becoming fixed, or in the case of some of the fur-fleas, to locate a second one after leaving the first to lay eggs, etc. In the case of hypodermal or sticktight fleas with ready access to hosts, to which they remain affixed for life, the pleural arch is greatly reduced. Those of diurnal hosts have large eyes. In contrast, are the nest-fleas, marked by reduction of eyes, combs, chaetotaxy, and thorax, as we have seen, and which presumably glue their eggs to debris in the nest rather than deposit them loosely among the hairs of the host. It should be borne in mind that fleas which are closely related taxonomically may vary considerably with respect to habit (and, accordingly, in habitus, to some degree). This is at times true of species placed in the same genus, e.g. *Chimaeropsylla* Rothschild, 1911 (xi.1) and also *Ceratophyllus* (iii.1). As N. C. Rothschild (1911) and Smit (1952) pointed out, *Chimaeropsylla potis* Rothschild, 1911 is modified as a sticktight flea, as indicated by the presence of broad, coarsely serrate laciniae and modifications in the head, in which the frontoclypeal region is shortened and the genal region lengthened. With a head of this type, the anchoring mouthparts may be swung in position as to be almost horizontal when embedded in the host, and be remote from the maxillary palpi. In contrast, in *Chim. haddowi* Smit, 1952, as that author has shown, the head is rounded, the genal-frontoclypeal regions are of comparable size and the stylets are narrow, suggesting this species is not truly a sticktight flea. The amplitude of swing of the mouthparts of *C. haddowi* is too great for a normal free-living flea, however, and hence Smit believes that species is tending towards "a sedentary life".

M. Rothschild & Hinton (1968) provide interesting support for Smit's belief that *C. potis* is a sticktight flea but *C. haddowi* is not, and this evidence is based upon their demonstration of a significant correlation between special adhesive discs on the antenna of male fleas and the degree of fixation of the female. During copulation, males of most species grasp the abdomen of the female by means of their elevated, long antennae, and Rothschild & Hinton believe that the discs help restrain the female during the act. These adhesive holding-structures have been noted in all but one of the recognized families of fleas (but not necessarily in all representatives thereof), and they are apparently well developed in species in which the females are active and mobile at the time of pairing. In the sessile fleas whose mating-habits have been observed, either the male antennae cannot be employed to grasp the female because of their structure and position, or else they lack the adhesive discs. Thus, in the European rabbit-flea, *Spilopsyllus cuniculi* (ix.1) the males grasp the females by their antennae while mating, but they lack the adhesive discs, as do the related species of the New World rabbit-fleas of the genus *Cediopsylla* Jordan, 1925. It is noteworthy that these female rabbit-fleas are essentially sessile at the time of mating. What is particularly relevant to the case of *Chimaeropsylla* is that the adhesive discs are lacking in *C. potis* but present in *C. haddowi*, as Rothchild & Hinton point out.

As M. Rothschild has stated (*in litt.*) the convergence between *Spilopsyllus* (and *Cediopsylla* as well) and *C. potis* is quite striking. In all three taxa, the frons is angled, the laciniae are stout and markedly serrate and the cuticula is dorsally incrassate and at times leathery elsewhere. All of these features are often seen in sticktight fleas. The 3 genera also agree in that both genal and prothoracic ctenidia are present, the eye is relatively large and the pleural arch is well developed. The last two features are characteristic of fleas of active diurnal hosts, and the chunky, stout body seen in these genera also suggests species that must seek such a host, just as the ctenidia recall the need to remain thereon once it is found, before the fleas become semi-sessile.

Fleas of the genus *Ceratophyllus* are particularly instructive in that marked behavioural and structural differences may occur even amongst species parasitizing the same kind of host, and hence the swallow-fleas of this genus are discussed in some detail.

Darskaya (1954b, 1959, 1964a) in a series of interesting articles on the subject, has classified the Palaearctic ceratophyllid bird-fleas into two ecological groups on the basis of the correlation of the behaviour of the fleas with the habits of the particular birds they parasitize. On the one hand are the "settled" fleas, which have a relatively pronounced host-specificity and can survive long periods of starvation in the nest after the birds have reared their young in the spring and have all departed. These are epitomized by the swallow-nest fleas which are poor jumpers and do not emigrate. Since the hosts of these fleas seldom alight, and even feed while flying, the inability of these fleas to leap well, and their disinterest in leaving the nest burrows, are adaptive advantages. If fleas of this class ever did fall to the ground, away from the nest-site, they would have virtually no chance of finding their specific hosts nor of returning to the nest. In the spring, however, some of these fleas may be carried by the birds from one nest or colony to another, before the birds settle down for nesting, but this particular kind of flea does not remain on the host for long periods.

During the spring and summer, the "settled" fleas generally produce only one generation. Possession of a very large fat-body, with stored nutriment, enables them to survive the long period (as much as 10 months) while they are nest-bound in the absence of the birds. During the winter, their body-functions are slowed as the fleas remain inactive in cracks in the nest. With the onset of warm weather in the spring, and the annual return of the birds, the fleas become very active, suck blood from the host avidly and quickly and rapidly mate and produce eggs. The larval stage is accelerated so the life-cycle is completed while the birds are still in the nest, giving the new crop of adults time to engorge on blood before the long siege begins. Inasmuch as the young birds likewise develop rapidly, and these birds have only one brood a year, an abbreviated span for the reproductive and developmental stages is a necessity.

Morphologically, the "settled" fleas are light in pigmentation or exhibit the characteristic banded appearance reported by Holland (1952) for *C. arcuegens*°. This is due to the anterior portions of the abdominal segments (both terga and sterna) being well sclerotized, or even especially so, while the posterior regions are lightly tanned. The former attribute offers protection to the body when the flea crawls into tight crevices in the nest; the latter permits gross enlargement of the abdomen as the fat-body enlarges. The alternating brown and light bands on the abdomen often enables one to recognize the specimens as bird-fleas even with the naked eye. This group of fleas is also characterized by relatively small (but nevertheless well developed) eyes, reduction or loss of sclerotization of the metanotal flange or "collar" (permitting flexibility of the abdomen in crawling, and scope in enlarging) and reduction or loss of the pleural arch, with concomitant lessened ability to jump and increased facility to crawl into crevices. Many of these attributes have been shown above to be characteristic in general of nest-fleas, and as indicated by Holland (1952) and Darskaya (1964a, b). Examples of fleas of this type are *C. delichoni*°, which lacks the pleural arch and *C. hirundinis*, in which it is present.

In contrast to the "settled" fleas are the bird-fleas which Darskaya calls "nomadic" or "migrating" (1954a, 1959, 1964a). (Perhaps in English, "perambulatory" may be a better term, avoiding the connotation of a fixed direction or a return, and yet indicate a purpose for the movement.) In this category are *C. garei* Rothschild, 1902 and *C. gallinae* (Schrank, 1803) which usually parasitize birds which do not return to utilize nests of the previous year, and hence any fleas which had hatched out in such a nest are faced with the problem of finding a bird to infest. This is solved by leaving the nest and actively seeking a host. *C. styx* (whose host, the sand-martin, generally does return to its old nest-site in the spring) leave the burrows in which they were born and may travel as much as 50 feet to another and new nest-site, "recognize" it, and settle there (Bates, 1962; M. Rothschild, 1969). This species, which is an excellent jumper and can span 200 mm (M. Rothschild, 1969), has the facility of immediately leaping onto a bird which hovers for a few seconds near the nest, and it seems likely that other bird-fleas can act similarly.

Perambulatory fleas usually have the ability to feed on a variety of hosts, enabling them to effectively parasitize nearly any bird they find. It is not surprising that fleas which have to be highly mobile to survive are: 1. excellent jumpers and climbers and fast walkers; 2. have large eyes; 3. well developed thoraces, including a large pleural arch; and 4. are almost black in colour due to the heavy tanning of the cuticle. The "nomadic" fleas overwinter in the cocoons and must feed soon after emergence or starve. The fat-body is small and is rapidly consumed during the summer, and the fleas feed frequently and quickly. Several generations are produced a year, since the hosts also tend to raise more than one litter annually. The flea-population in such nests can build up to enormous proportions.

Darskaya's notable observations were necessarily based upon study of a limited number of species of *Ceratophyllus* in the U.S.S.R. and dealt with a variety of complex and little-known phenomena. Even so, her generalizations, in the main, apply well to bird-fleas from other parts of the world and to other taxa, as will be shown shortly. As is to be expected, however, some species that have certain of the attributes of "nomadic" fleas exhibit a pattern of behaviour somewhat different from that of *C. garei*, etc. For example, they conform with respect to the morphological features noted above and in that these fleas appear to spend little or no time in the nests as adults, and actively seek their hosts. These fleas, however, apparently spend most of their adult lives on the birds themselves and hence, as pointed out by M. Rothschild (*in litt.*) are analagous to the "body-fleas" or "fur-fleas" of mammals. Such fleas presumably can accompany a bird on migrations of thousands of miles. Thus, the Holarctic *Dasypsyllus gallinulae* (Dale, 1878) (iii.1) has not only been found in North America and Europe but in such extremes as Panama and the Far North, and in regions as distant as the Philippines (Traub, 1950b), North Borneo and Malaya. I was surprised to collect the "arctic" species *Dasypsyllus stejnegeri* (Jordan, 1929) in central Mexico, but Smit (1961) reported it from the Falkland Islands! The Panama records of *D. gallinulae* were based upon specimens Dr. H. C. Matthes collected from a sudden infestation on his own body, while walking in the forest of Mt. Volcán. It therefore seems likely that this is a perambulatory species.

In all probability, other bird-fleas, whose habits have not yet received the type of intensive study undertaken by Darskaya for Palaearctic *Ceratophyllus*, could be divided into similar ecologic groups. The Antarctic flea, *Glaciopsyllus*° and the spilopsylline fleas of sea-birds are in the category of "settled" fleas, as indicated above. *Lentistivalius insolli* (ii.1) with its brown and white banded appearance relatively small eye and records of collections from nests rather than birds, presumably is in this category. Fleas of the genus *Hoogstraalia*, which possess a genal ctenidium, and are darker in colour, etc., may be "perambulatory" fleas.

Although the ecology of rodent-fleas has not been studied as well as that of bird-fleas, because of the inherent difficulties, a great deal of fine work has been done in the Soviet Union on this subject. It is apparent that the behaviour of the rodent-fleas is as specialized and complex, and as inter-related with the habits of the host as the bird-fleas mentioned above. For example, several species of fleas with well developed eyes have been noted to swarm to and about the burrow-opening, pursue prospective hosts or "emigrate" into new burrows if their birth-places had been abandoned by the rodents (Darskaya, 1954a, 1955, 1964b; Ioff, 1941).

K. The Principle of Structural Compensation

It has been pointed out that in Siphonaptera the total mass of two or more structures that are associated in a common function generally is a theoretical constant (Traub, 1969). For example, the claspers, which operate as a unit in grasping the female in copulation, may be of approximately equal size, or else the movable finger (F.) may be enlarged while the immovable process (P.) is small, or thirdly, F. may be reduced and P. huge. It was also shown that the relative size of Ford's sclerite varies inversely with the comparative degree of development of the crochets or of ventral paramere-like processes. In other words, although the size of the individual components may vary, they do so inversely, in a correlated manner, and, in effect, the total amount of tissue-substance involved is the same, and the over-all functional result is apparently not impaired. The specimens collected by Lord Medway's team on Gunong Benom, and the other material discussed in the previous article in this series (Traub, 1972a), also provide interesting examples of this principle.

Particularly relevant are the unusual specializations cited and illustrated for each sex of *Stivalius cognatus* Jordan & Rothschild, 1922 (a member of *Stivalius* Jordan & Rothschild, 1922 *s. str.*). It will be recalled that in the previous article it was emphasized how the sclerotized inner tube (S.I.T.) is characteristically elongated in that taxon and that Ford's sclerite (F.SC.) is greatly enlarged, while, in contrast, the paramere-like ventral process of the crochet is vestigial or totally absent. The situation is very different in most members of *Stivalius s. lat.*, which have well developed ventral crochet-processes (CR.P.), and in which S.I.T. is short and broad in comparison, i.e. *Medwayella* and *Lentistivalius*, as figured in that article. It was therefore suggested that the hypertrophied Ford's sclerite and highly elongate S.I.T. serve to replace, in function, the ventral "parameres," which have been lost in the course of evolution. That the reduction of CR.P. and concomitant modifications of S.I.T. and of F.SC. are in accord with this principle of structural compensation is further suggested by developments in other members of *Stivalius s. lat.*, viz. *S. jacobsoni* Jordan & Rothschild, 1922 and *Parastivalius novaeguineae* (Rothschild, 1904). These two are in the minority of "*Stivalius*" in which the aedeagus lacks ventral caudad-directed, finger-like or rectangular processes, and in each case there is a unique alternate device that appears as an apparent substitute. Thus, *S. jacobsoni* is one of the few species in which the very apex of the dorsal wall of the end-chamber of the aedeagus is highly modified, in this case being produced into 2 highly acuminate fang-like projections. In *P. novaeguineae*, the ventral armature of S.I.T. is not only displaced far caudad, but it is hook-like suggesting a crochet in appearance.

If the principle of structural compensation is a sound one, then it would be expected that there would be intermediate species in which the cooperating members of the functional device were only partially modified, e.g. there would be varying degrees of development of alternate mechanisms. *S. phoberus* (Rothschild, 1904) is an example of such an intermediate form, since, as has been shown in the previous article in this series, S.I.T. is not nearly as elongate as in other members of the genus (*Stivalius s. str.*), and the vestige of the crochet-process (CR.P.) is longer than in its allies. What then compensates for the loss of the functional part of CR.P., the ventral caudad-directed "parameres"? It is noteworthy in this regard that several of the associated sclerites seem more highly developed in *S. phoberus* than in related fleas with the ophidian-like S.I.T. Thus: (1) F.SC. bears 2 apical hooks per side, not 1. (2) S.I.T. has a longer and broader apical fistula (FIS.) which is tanned to a greater degree than in *S. cognatus*, etc. FIS. in *S. phoberus* also appears to have more discreet tanned borders *within* S.I.T. (and may prove to be protrusible, at least here, if not throughout the genus).

Another relevant example of the principle of compensation is provided by the metasternal furca, as has been indicated by M. Rothschild (*in litt.*). In fleas which have lost the pleural arch, the furca is hypertrophied, as in the case of *Wenzella*° (fig. 85, I.F.-3) and *Conorhinopsylla*° (fig. 86). This tendency is even exhibited in members of the same genus which differ with respect to the development of the pleural arch and ridge, e.g. *Opisodasys* and *Ceratophyllus*, and is presumably associated with the attachment of muscles which ordinarily fasten to the pleural ridge when the arch is present.

The principle of compensation actually seems to apply to more than adjacent or cooperating structures or organs, for the extreme modifications of the hypodermal and sessile fleas (Tunginae) presumably fit the concept. Here the head and mouthparts have become enlarged or greatly strengthened, and the abdomen capable of enlarging enormously, while the thorax has become so tremendously compressed that it is difficult to discern its components.

The Principle of Structural Compensation is a corollary of the Principle of Totality of Mass (Traub, 1969), which states that while the components of a structure may vary in size or mass, the over-all size is a relative "constant". Thus, in some species the pronotal spines are long, while the pronotum is narrow, as in figs 18 and 21; in others, the reverse is true (fig. 63). The latter principle is well illustrated by a species treated above as an example of a flea undergoing reduction of ctenidia, namely *Trichopsylloides oregonensis*°. Here the genal ctenidium is usually entirely absent, or else is represented by but 1 or 2 tiny pale spines. It is noteworthy that the gena itself is unusually large and overlaps the base of the procoxa. It thus encompasses the same area as does the fully developed comb of the related genus *Rhadinopsylla*°.

V. CONCLUSIONS

Fleas are far more specialized for their particular mode of life than had been realized a few years ago, not only with respect to their behaviour and physiological responses, but also concerning their morphology. All of these phenomena are intimately related to corresponding features of their host and bespeak of an ancient and intimate association between parasite and host, even to the point of evolving together, as witness the fit of the pronotal combs of some fleas to the hairs of the mammal they infest. In other instances, the pronotal comb and structure of the thorax and degree of development of the eye, reflect the environment and habits of the host and the corresponding modifications of the flea thereto.

The adaptive responses of the Siphonapteran pronotal comb to the pattern of the hairs of the host, and the association between the structure of the metathorax and the advantages or disadvantages of the ability to leap, are examples of the moulding-influence of the environment, which tends to result in uniformity of physiognomy, despite the fact that different mechanisms may have been employed to achieve these ends. Such modifications in fleas therefore parallel the remarkable convergences seen almost everywhere in nature, viz., the amazing similarity in appearance of carnivorous marsupials and the placentate Carnivora even though the two represent two independent lines of evolution.

It is apparent that there still is a great deal to be learned about some of the principles involved in the examples of convergent evolution and adaptations mentioned, to say nothing of the details. Some of the many unanswered questions could be resolved if more were known about the flea-fauna of South America, Australia and the Australo-Indonesian Archipelago, and about host-relationships in general. Even more, we require data on the ecology of fleas and mammals and birds, and study of living material.

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VII. LIST OF TAXA CITED IN TEXT

Code	*Family*	*Code*	*Subfamily*
i.	Hystrichopsyllidae	1	Hystrichopsyllinae
		2	Anomiopsyllinae
		3	Ctenophthalminae
		4	Dinopsyllinae
		5	Doratopsyllinae
		6	Listropsyllinae
		7	Neopsyllinae
		8	Rhadinopsyllinae
		9	Stenoponiinae
ii.	Pygiopsyllidae	1	Pygiopsyllinae
		2	Lycopsyllinae
iii.	Ceratophyllidae	1	Ceratophyllinae
		2	Foxellinae

iv.	Leptopsyllidae	1	Leptopsyllinae
		2	Amphipsyllinae
v.	Ischnopsyllidae	1	Ischnopsyllinae
		2	Thaumapsyllinae
vi.	Rhopalopsyllidae	1	Rhopalopsyllinae
		2	Parapsyllinae
ix.	Pulicidae	1	Pulicinae
		2	Tunginae
x.	Vermipsyllidae		—
xi.	Chimaeropsyllidae	1	Chimaeropsyllinae
		2	Chiastopsyllinae
xiii.	Coptopsyllidae		—
xiv.	Malacopsyllidae		—
xv.	Xiphiopsyllidae		—

Code	*Genus or Species*	*Page*
ii.1	*Acanthopsylla* Jordan & Rothschild, 1922	339, 341
iv.2	*Acropsylla* Rothschild, 1911	351
iv.2	,, *girshami* Traub, 1950	F50
ix.1	*Actenopsylla* Jordan & Rothschild, 1923	328, 362
ix.1	,, *suavis* Jordan & Rothschild, 1923	328, 342, 348, F99
iii.1	*Aenigmopsylla grodekovi* Sychevsky, 1950	314, F9
i.3	°*Agastopsylla* Jordan & Rothschild, 1923	325, 333, 352
iv.2	*Amphipsylla* Wagner, 1909	327, 331, 347
iv.2	,, *marikovskii* Ioff & Tiflov, 1939	327, 333, F100, F101, F102
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i.2	°*Anomiopsyllus* Baker, 1904	324, 329, 333, 345, 352, 354, 355
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v.1	°*Araeopsylla* Jordan & Rothschild, 1921	333
ix.1	*Archaeopsylla* Dampf, 1908	320
iv.2	°*Brachyctenonotus* Wagner, 1928	327, 333, 352
ii.1	*Bradiopsylla* Jordan & Rothschild, 1922	341
ii.1	,, *echidnae* (Denny, 1843)	320
iii.1	*Brevictenidia* Liu & Li, 1965	341, 352
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iv.2	*Caenopsylla* Rothschild, 1909	331
iv.2	,, *laptevi* Mikulin & Zagniborodova, 1958	F71
iv.2	°*Calceopsylla* Liu, Wu & Wang, 1965	327, 333, 352
i.2	°*Callistopsyllus* Jordan & Rothschild, 1915	324, 333, 335
iii.1	*Callopsylla* Wagner, 1934	356
iii.1	,, *dolabris* (Jordan & Rothschild, 1911)	326, 356, F84
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i.7	,, *charlottensis* (Baker, 1898)	321, F67
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ix.1 *Centetipsylla* Jordan, 1925 320
iii.1 *Ceratophyllus* Curtis, 1832 326, 334, 355, 363, 364, 366, 368
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iii.1 *Citellophilus* Wagner, 1934 356
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i.3 ,, *(Nearctoctenophthalmus) haagi* Traub, 1950 . . F26
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° The °, if applicable, precedes the name in this List for convenience in scanning, whereas in the text it follows the name.

VIII. LIST OF HOSTS

Allactaga Cuvier, 1836
Aplodontia Richardson, 1829
Apodemus Kaup, 1829
Arctictis binturong (Raffles, 1821)
Arvicanthis Lesson, 1842
Bathyergus Illiger, 1811
Callosciurus Gray, 1867
,, *erythraeus* (Pallas, 1778)
Calomyscus Thomas, 1905
Citellus Oken, 1816
,, *dauricus* Brandt, 1843
Cryptomys Gray, 1864
Cynomys Rafinesque, 1817
Dremomys Heude, 1898
Erinaceus Linnaeus, 1758
Eutamias Trouessart, 1769
Felis bengalensis Kerr, 1792
Heteromys Desmarest, 1817
Hylopetes Thomas, 1908
Hyperacrius Miller, 1896
Lariscus Thomas & Wroughton, 1867
Marmota Blumenbach, 1779
Martes Pinel, 1792
Meriones Illiger, 1811
Microtus Schrank, 1798
Mus Linnaeus, 1758
Myospalax Laxmann, 1769
Neotoma Say & Ord, 1825
Neotomodon Merriam, 1898
Ochotona Link, 1795
Octomys Thomas, 1920
Onychomys Baird, 1857
Oryzomys Baird, 1857
Otomys unisulcatus Cuvier & Geoffroy, 1829
Peromyscus Gloger, 1841
Petaurus Shaw & Nodder, 1791
Petrochelidon Cabanis, 1850
Pogonomys Milne-Edwards, 1877
Ptychorhamphus M. Brandt, 1837
Puffinus Brisson, 1760
Rattus Fischer, 1803
Rattus (*Rattus*) Fischer, 1803
Reithrodontomys mexicanus Saussure, 1860
Rhinosciurus Gray, 1843
Rhombomys Wagner, 1841
Romerolagus Merriam, 1896
Sciurus Linnaeus, 1758
,, *granatensis chiriquensis* Bangs, 1902
Spalax Guldenstaedt, 1770
Tachyglossus Illiger, 1811
Tamias, Illiger, 1811
Tamiasciurus Trouessart, 1880
Tupaia Raffles, 1821

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Vision, 346–351, 364–366
Volcano-Rabbit, 358
Vole, 337, 347, 351

Weasel, 357
Wolf, 357
Wombat, 325, 326
Woodpecker, 346

Xenopsyllines, 354

Zoogeographic Notes, 354–357

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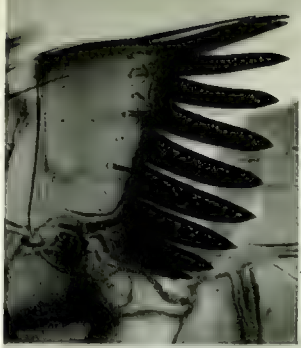
PLATE 1

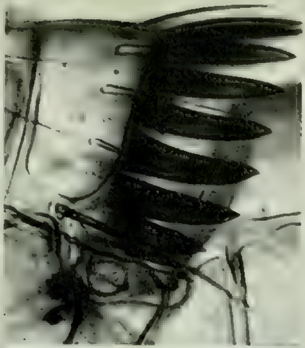
Fleas of Tree-Squirrels

FIG. 1. (iii.1) *Monopsyllus vison* (Baker, 1904) Nearctic
FIG. 2. (iii.1) *Orchopeas h. howardi* (Baker, 1895) Nearctic
FIG. 3. (iii.1) *Syngenopsyllus calceatus* (Rothschild, 1905) Indo-Malaysian
FIG. 4. (i.2) *Megarthroglossus divisus exsecatus* Wagner, 1936 Nearctic
FIG. 5. (iii.1) *Opisodasys robustus* (Jordan, 1925) Nearctic
FIG. 6. (ii.1) *Medwayella robinsoni* (Rothschild, 1905) Indo-Malayan
FIG. 7. (iii.1) *Macrostylophora fimbriata* (J. & R., 1921) Himalayan
FIG. 8. (iii.1) *Tarsopsylla octodecimdentata* (Kolenati, 1863) Palaearctic

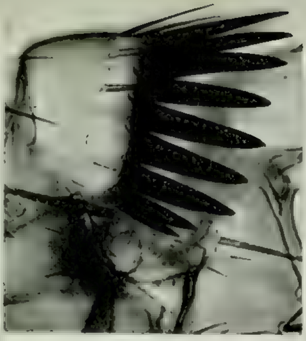
FLEAS OF TREE-SQUIRRELS



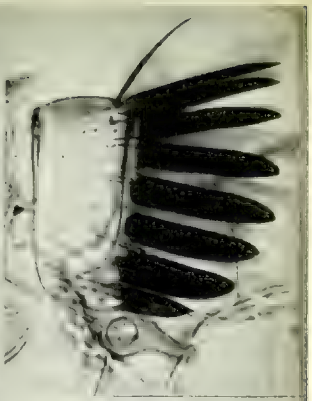
1 (III.1) MONOPSYLLUS VISON (BAKER, 1904) NEARCTIC



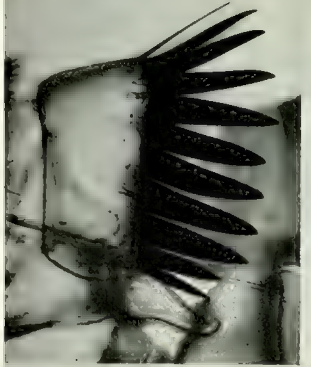
2 (III.1) ORCHOPEAS H. HOWARDI (BAKER, 1895) NEARCTIC



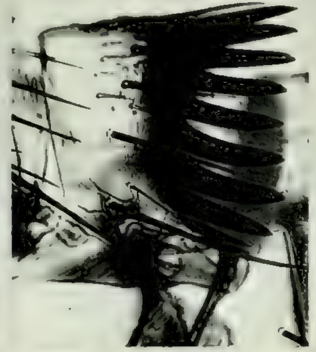
3 (III.1) SYNGENOPSYLLUS CALCEATUS (ROTHSCHILD, 1905) INDO-MALAYSIAN



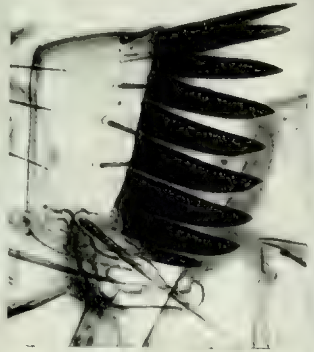
4 (I.2) MEGARTHROGLOSSUS DIVISUS EXSECATUS WAGNER, 1936 NEARCTIC



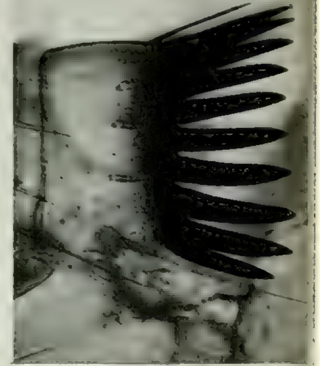
5 (III.1) OPISODASYS ROBUSTUS (JORDAN, 1925) NEARCTIC



6 (II.1) MEDWAYELLA ROBINSONI (ROTHS., 1905) INDO-MALAYAN



7 (III.1) MACROSTYLOPHORA FIMBRIATA (J & R., 1921) HIMALAYAN

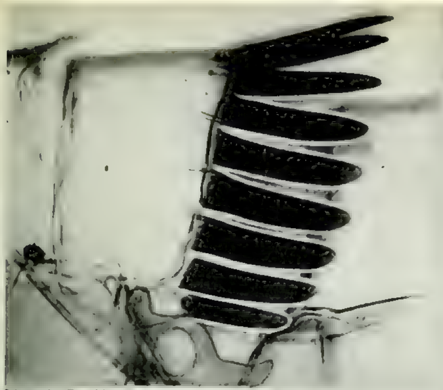


8 (III.1) TARSOPSYLLA OCTODECIMDENTATA (KOLENATI, 1863) PALAEARCTIC

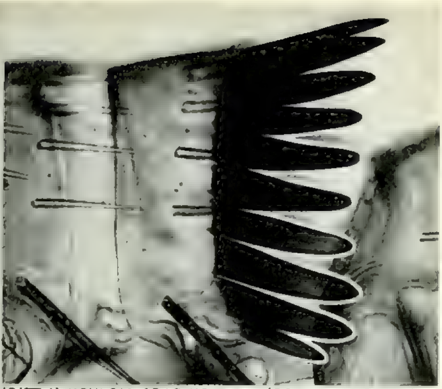
PLATE 2

Fleas of Tree-Squirrels

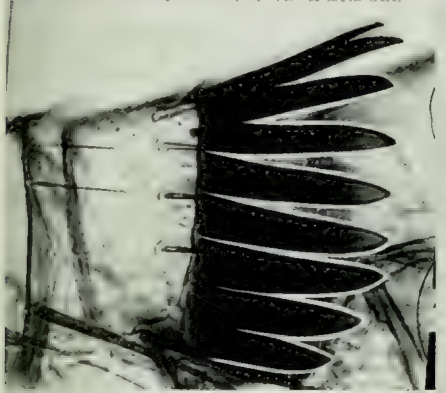
FIG. 9. (iii.1) *Aenigmopsylla grodekovi* Sychevsky, 1950 Palaearctic
FIG. 10. (iii.1) *Kohlsia graphis* (Rothschild, 1909) Central America
FIG. 11. (iii.1) *Nosopsyllus ceylonensis* Smit, 1953 Ceylon
FIG. 12. (iii.1) *Pleochaetis soberoni* Barrera, 1958 Mexico
FIG. 13. (iii.1) *Libyastus infestus* (Rothschild, 1908) Ethiopian
FIG. 14. (iii.1) *Macrostylophora hastata* (J. & R., 1921) Indo-Malayan



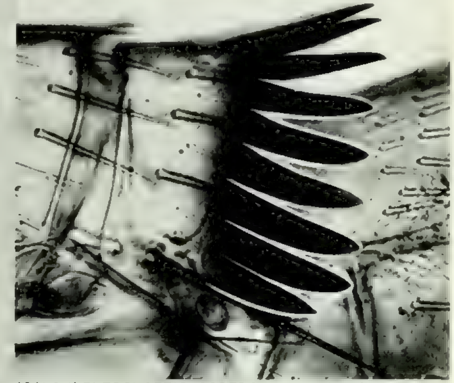
9(III.1) AENIGMOPSYLLA GRODEKOVI SYCHEVSKY, 1950
PALAEARCTIC



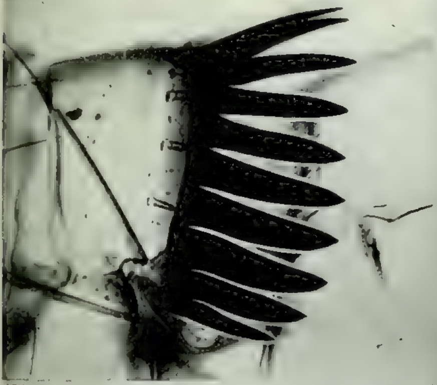
10(III.1) KOHLSIA GRAPHIS (ROTHSCHILD, 1909)
CENTRAL AMERICA



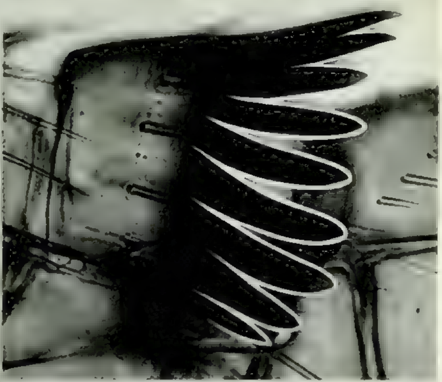
11(III.1) NOSOPSYLLUS CEYLONENSIS SMIT, 1953
CEYLON



12(III.1) PLEOCHAETIS SOBERONI BARRERA, 1958
MEXICO



13(III.1) LIBYASTUS INFESTUS (ROTHSCHILD, 1908)
ETHIOPIAN



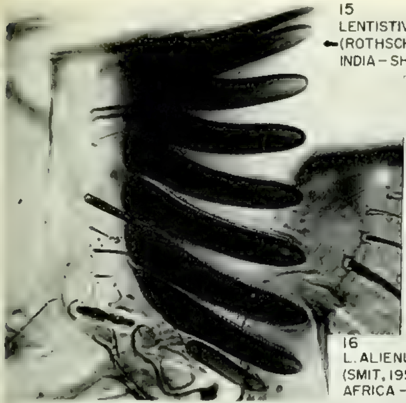
14(III.1) MACROSTYLOPHORA HASTATA (J. & R., 1921)
INDO-MALAYAN

FLEAS OF TREE-SQUIRRELS

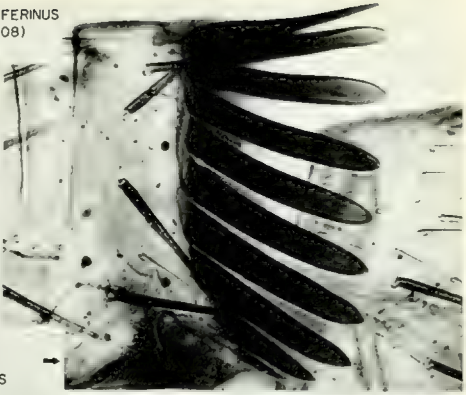
PLATE 3

Variations in Pronotal Combs—**Lentistivalius** and an Allied Taxon (ii.1)

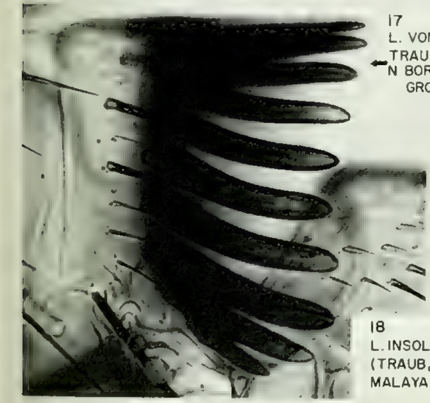
Fig. 15. *Lentistivalius ferinus* (Rothschild, 1908) India—Shrews
Fig. 16. *L. alienus* (Smit, 1958) Africa—Murids
Fig. 17. *L. vomerus* Traub, 1972 N. Borneo—*Tupaia* and Ground-Squirrels
Fig. 18. *L. insolli* (Traub, 1950) Malaya—Birds
Fig. 19. *L. aestivalis* (Jameson & Sakaguti, 1954) Japan—*Apodemus*
Fig. 20. *Stivalius klossi* (Jordan & Rothschild, 1922) Indo-Malaysian—*Rattus*



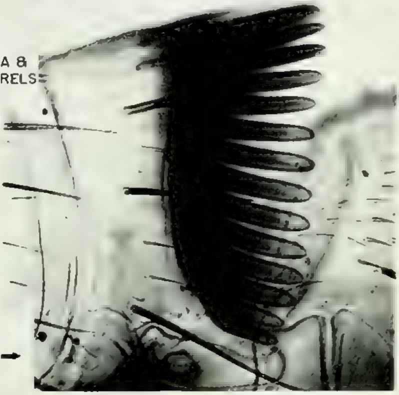
15
LENTISTIVALIUS FERINUS
(ROTHSCHILD, 1908)
INDIA – SHREWS



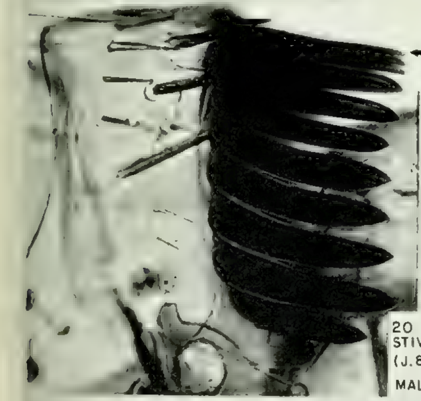
16
L. ALIENUS
(SMIT, 1958)
AFRICA – MURIDS



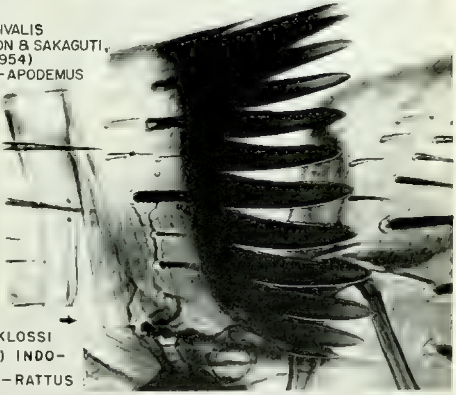
17
L. VOMERUS
TRAUB, 1971
N BORNEO – TUPAIA &
GROUND-SQUIRRELS



18
L. INSOLLI
(TRAUB, 1950)
MALAYA – BIRDS



19
L. AESTIVALIS
(JAMESON & SAKAGUTI,
1954)
JAPAN – APODEMUS



20
STIVALIUS KLOSSI
(J. & R., 1922) INDO-
MALAYSIAN – RATTUS

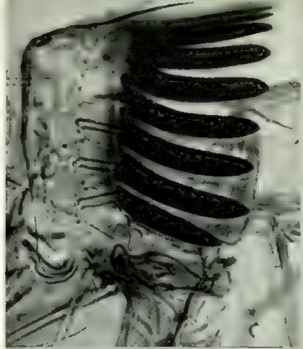
VARIATIONS OF PRONOTAL COMBS – LENTISTIVALIUS
AND AN ALLIED TAXON (II.1)

PLATE 4

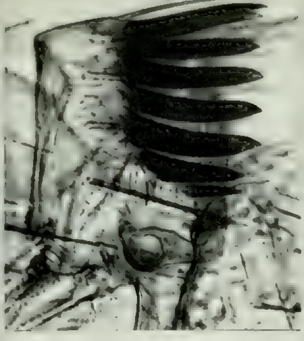
Variations in Pronotal Combs—**Ctenophthalmus** (i.3)

FIG. 21. *C. expansus myodosus* Traub & Barrera, 1966 Mexico—Shrews
FIG. 22. *C. a. agyrtes* (Heller, 1896) Palaearctic—Voles, etc.
FIG. 23. *C. pollex* Wagner & Ioff, 1926 U.S.S.R.—*Citellus*
FIG. 24. *C. bisoctodentatus* Kolenati, 1863 Palaearctic—Talpids
FIG. 25. *C. cryptotis* Traub & Barrera, 1966 Mexico—Shrews
FIG. 26. *C. haagi* Traub, 1950 Mexico—Voles
FIG. 27. *C. rettigi* Rothschild, 1908 U.S.S.R.—Cricetines
FIG. 28. *C. l. levanticus* Lewis, 1964 Middle East—*Spalax*

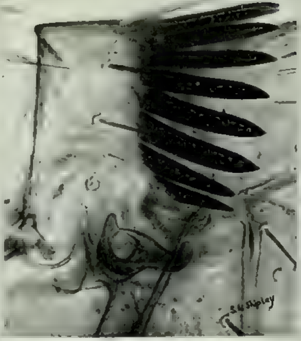
VARIATIONS IN PRONOTAL COMBS — CTENOPHTHALMUS (I. 3)



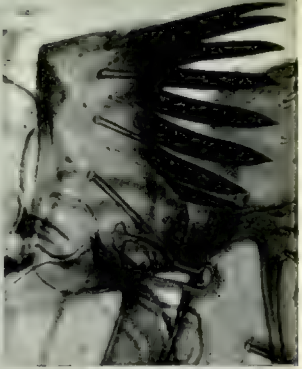
21 C. EXPANSUS MYODOSUS
TRAUB & BARRERA, 1966
MEXICO - SHREWS



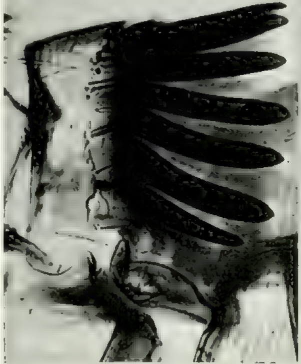
22 C. A. AGYRTES (HELLER, 1896)
PALAEARCTIC-VOLES, ETC.



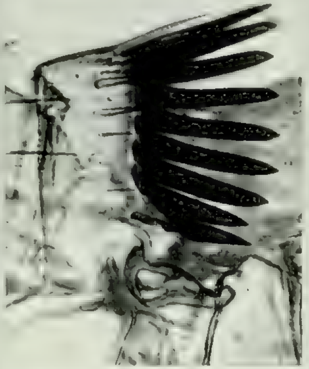
23 C. POLLEX
WAGNER & IOFF, 1926
U.S.S.R. - CITELLUS



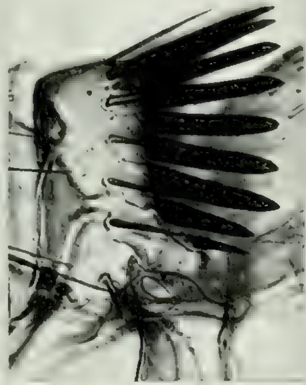
24 C. BISOCTODENTATUS
KOLENATI, 1863
PALAEARCTIC - TALPIDS



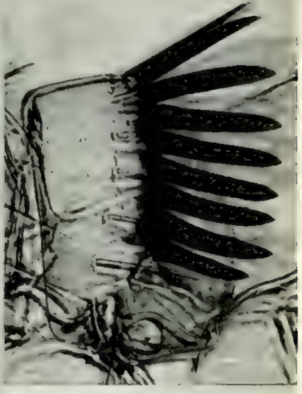
25 C. CRYPTOTIS
TRAUB & BARRERA, 1966
MEXICO - SHREWS



26 C. HAAGI TRAUB, 1950
MEXICO - VOLES



27 C. RETTIGI ROTHSCHILD, 1908
U.S.S.R. - CRICETINES



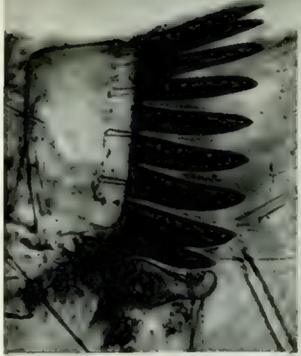
28 C. L. LEVANTICUS LEWIS, 1964
MIDDLE EAST - SPALAX

PLATE 5

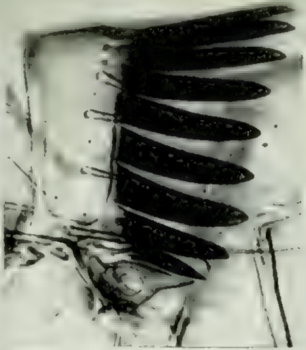
Variations in Pronotal Combs—**Orchopeas** (iii.1)

FIG. 29	*O. n. nepos* (Roths., 1905) Nearctic—Tree-Squirrels
FIG. 30	*O. sexdentatus agilis* (Roths., 1905) Nearctic—*Neotoma*
FIG. 31	*O. fulleri* Traub, 1950 Mexico—Tree-Squirrels
FIG. 32	*O. neotomae* Augustson, 1943 Nearctic *Neotoma*
FIG. 33	*O. caedens* (Jordan, 1925) Nearctic—Tree-squirrels
FIG. 34	*O. sexdentatus* (Baker, 1904) Nearctic—Desert *Neotoma*
FIG. 35	*O. bolivari* Barrera, 1955 Mexico—Flying-Squirrels (?)
FIG. 36	*O. leucopus* (Baker, 1904) Nearctic—*Peromyscus*

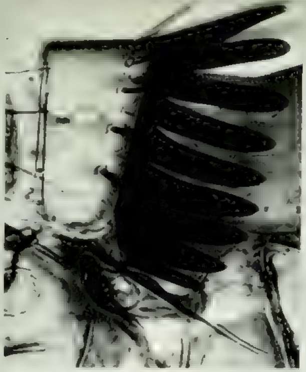
VARIATIONS IN PRONOTAL COMBS – ORCHOPEAS (III.1.)



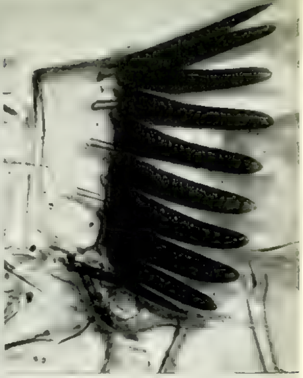
29 O. N. NEPOS (ROTHS., 1905)
NEARCTIC – TREE-SQUIRRELS



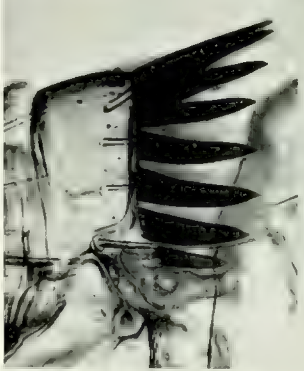
30 O. SEXDENTATUS AGILIS
(ROTHS., 1905)
NEARCTIC – NEOTOMA



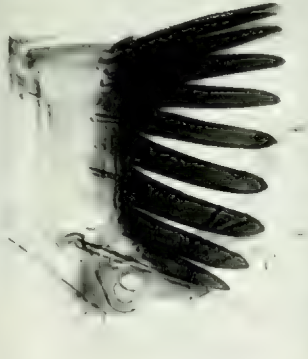
31 O. FULLERI TRAUB, 1950
MEXICO – TREE-SQUIRRELS



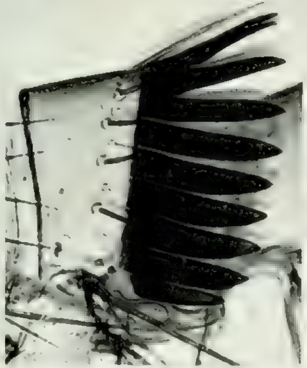
32 O. NEOTOMAE
AUGUSTSON, 1943
NEARCTIC – NEOTOMA



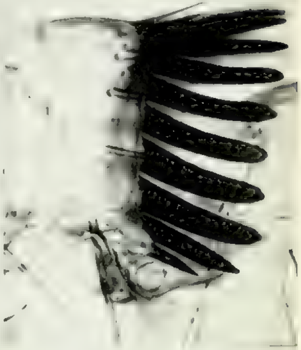
33 O. CAEDENS (JORDAN, 1925)
NEARCTIC – TREE-SQUIRRELS



34 O. SEXDENTATUS (BAKER, 1904)
NEARCTIC – DESERT NEOTOMA



35 O. BOLIVARI BARRERA, 1955
MEXICO – FLYING-SQUIRRELS (?)



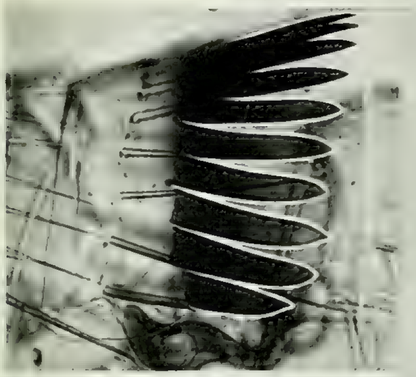
36 O. LEUCOPUS (BAKER, 1904)
NEARCTIC – PEROMYSCUS

PLATE 6

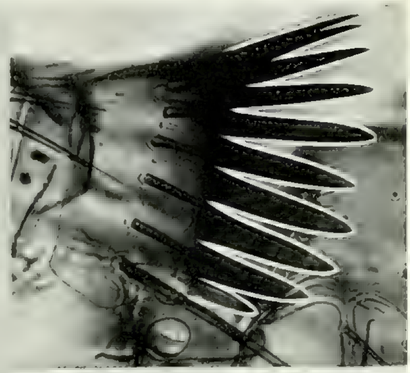
Pronotal Combs—Sciurid Fleas Versus Murine Fleas in Genus **Neopsylla**

FIG. 37 (i.7) *Neopsylla setosa* (Wagner, 1898) Palaearctic—Chipmunk
FIG. 38 (i.7) *Neopsylla luma* Traub, 1954 Borneo—*Rattus*
FIG. 39 (i.7) *Neopsylla inopina* Roths., 1915 Nearctic—Ground-Squirrels
FIG. 40 (i.7) *Neopsylla dispar* Jordan, 1932 Malaysian—*Rattus*
FIG. 41 (i.7) *Neopsylla bidentatiformis* (Wagner, 1893) Palaearctic—Cricetines & Ground-Squirrels
FIG. 42 (i.7) *Neopsylla hissarica* Ioff & Sosnina, 1950 Palaearctic—*Rattus*

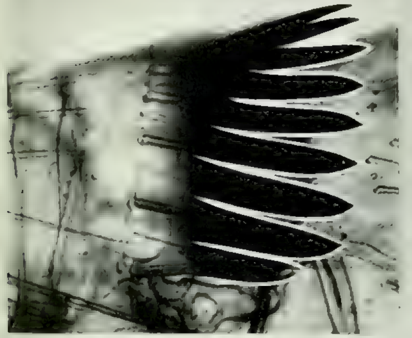
PRONOTAL COMBS – SCIURID FLEAS VERSUS MURINE FLEAS IN GENUS NEOPSYLLA



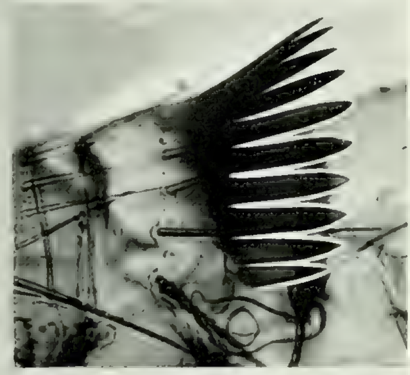
37 (I 7) NEOPSYLLA SETOSA (WAGNER, 1898)
PALAEARCTIC – CHIPMUNK



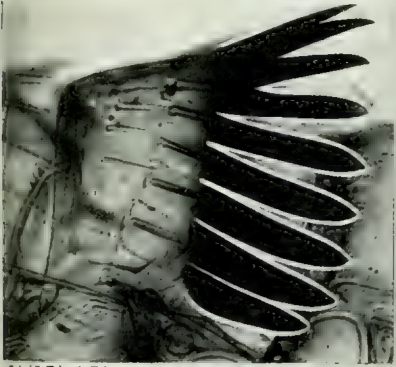
38 (I 7) NEOPSYLLA LUMA TRAUB, 1954
BORNEO – RATTUS



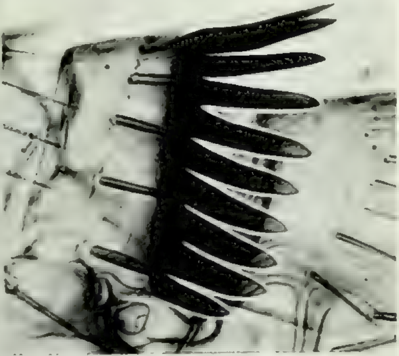
39 (I 7) NEOPSYLLA INOPINA ROTHS., 1915
NEARCTIC – GROUND-SQUIRRELS



40 (I 7) NEOPSYLLA DISPAR JORDAN, 1932
MALAYSIAN – RATTUS



41 (I.7) NEOPSYLLA BIDENTATIFORMIS
(WAGNER, 1893) PALAEARCTIC –
CRICETINES & GROUND-SQUIRRELS



42 (I.7) NEOPSYLLA HISSARICA
IOFF & SOSNINA, 1950
PALAEARCTIC – RATTUS

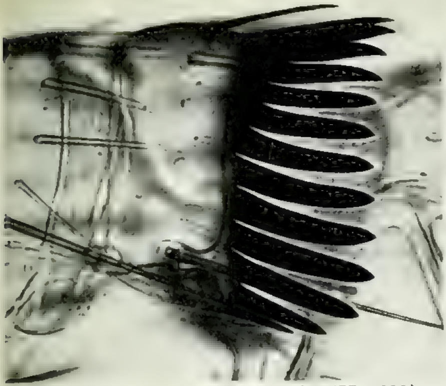
LIST OF ILLUSTRATIONS

PLATE 7

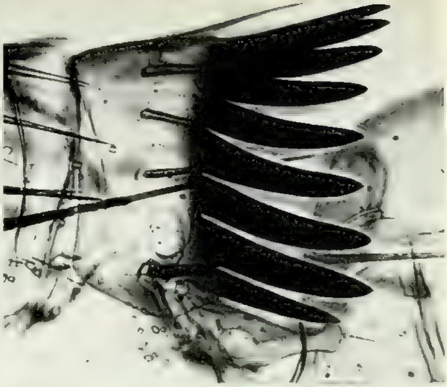
Pronotal Combs—**Opisodasys** (Nearctic)

FIG. 43 (iii.1) *Opisodasys keeni* (Baker, 1896) *Peromyscus*
FIG. 44 (iii.1) *Opisodasys hollandi* Traub, 1947 Tree-Squirrel
FIG. 45 (iii.1) *Opisodasys nesiolus* Augustson, 1941 *Peromyscus*
FIG. 46 (iii.1) *Opisodasys robustus* (Jordan, 1925) Tree-Squirrel
FIG. 47 (iii.1) *Opisodasys pseudarctomys* (Baker, 1904) Flying-Squirrel
FIG. 48 (iii.1) *Opisodasys enoplus* (Roths., 1909) Tree-Squirrel

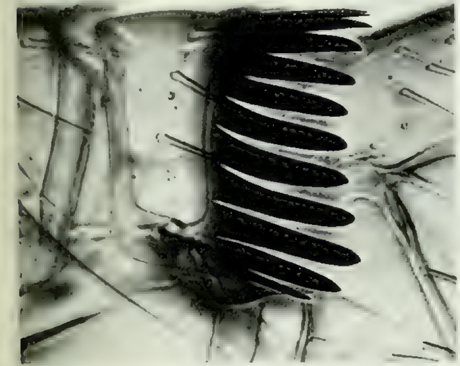
PRONOTAL COMBS – OPISODASYS (NEARCTIC)



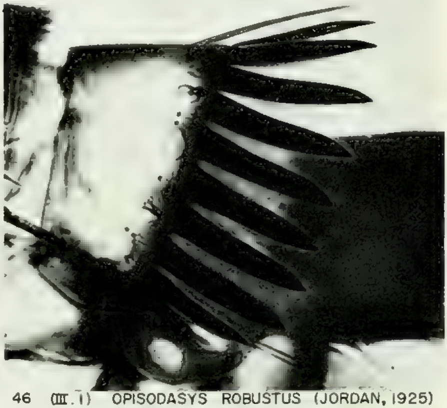
43 (III.1) OPISODASYS KEENI (BAKER, 1896)
PEROMYSCUS



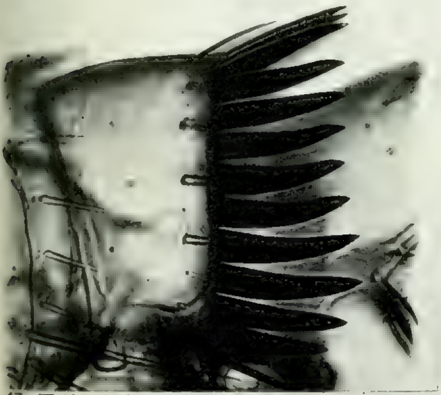
44 (III.1) OPISODASYS HOLLANDI TRAUB, 1947
TREE – SQUIRREL



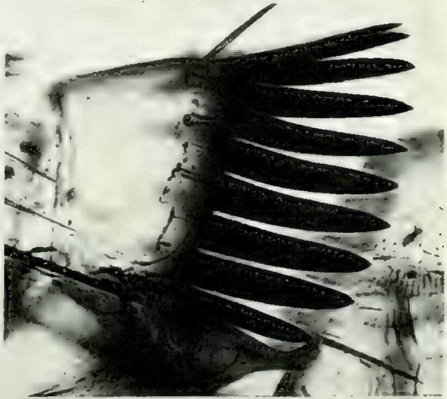
45 (III.1) OPISODASYS NESIOTUS AUGUSTSON, 1941
PEROMYSCUS



46 (III.1) OPISODASYS ROBUSTUS (JORDAN, 1925)
TREE – SQUIRREL



47 (III.1) OPISODASYS PSEUDARCTOMYS (BAKER, 1904)
FLYING – SQUIRREL



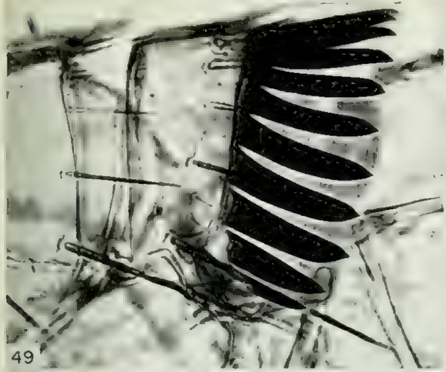
48 (III.1) OPISODASYS ENOPLUS (ROTHS., 1909)
TREE – SQUIRREL

PLATE 8

Pronotal Combs—Fleas of Murines

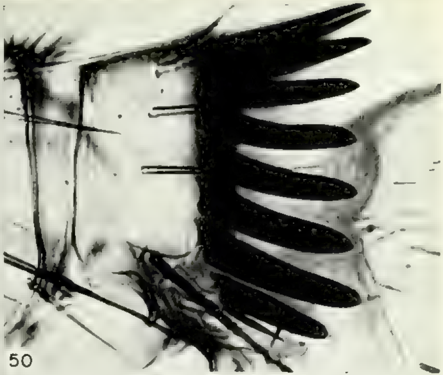
FIG. 49 (iii.1) *Nosopsyllus londiniensis* (Roths., 1903) Egypt (and introduced) –*Arvicanthis* and Rats
FIG. 50 (iv.2) *Acropsylla girshami* Traub, 1950 Eastern Palaearctic—*Mus*
FIG. 51 (ii.1) *Stivalius* (*Gryphopsylla*) *hopkinsi* Traub, 1957 Borneo—*Rattus*
FIG. 52 (ii.1) *Stivalius cognatus spiramus* Jordan, 1926 Philippines—*Rattus* (*Rattus*)
FIG. 53 (iv.1) *Leptopsylla pamirensis* (Ioff, 1946) Eastern Palaearctic—*Apodemus*
FIG. 54 (iv.1) *Sigmactenus alticola* Traub, 1954 Borneo—*Rattus* (*Rattus*)

PRONOTAL COMBS - FLEAS OF MURINES



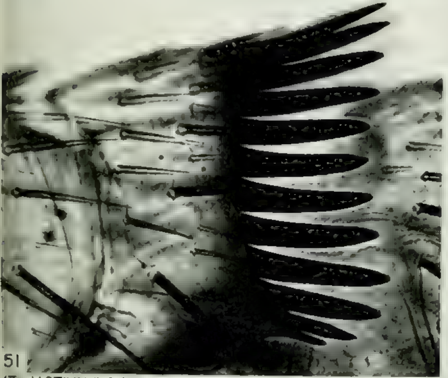
49

(III 1)NOSOPSYLLUS LONDINIENSIS (ROTHSCHILD, 1903)
EGYPT (AND INTRODUCED) - ARVICANTIS & RATS



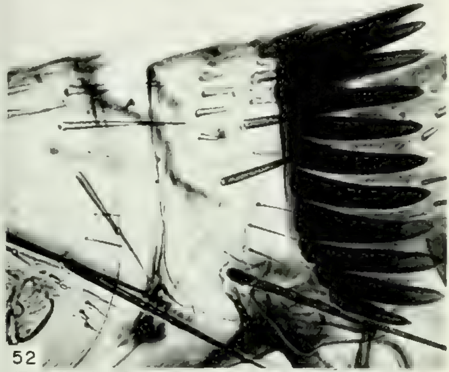
50

(IV 2)ACROPSYLLA GIRSHAMI TRAUB, 1950
EASTERN PALAEARCTIC—MUS



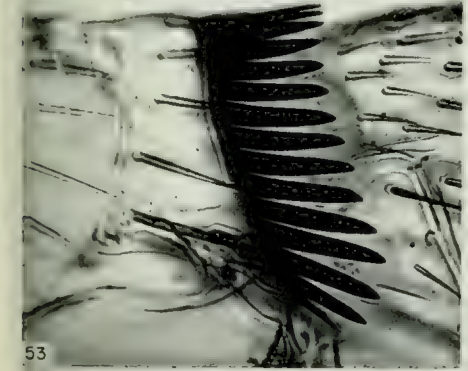
51

(II. 1)STIVALIUS (GRYPHOPSYLLA) HOPKINSI TRAUB, 1957
BORNEO—RATTUS



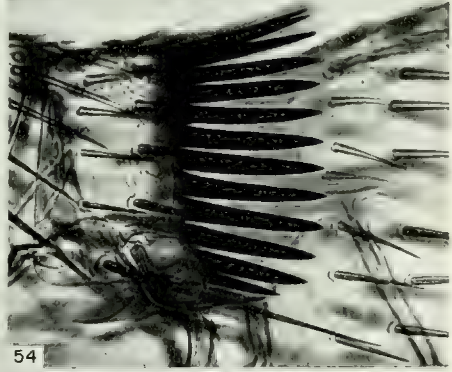
52

(II. 1)STIVALIUS COGNATUS SPIRAMUS JORDAN, 1926
PHILIPPINES—RATTUS (RATTUS)



53

(IV 1)LEPTOPSYLLA PAMIRENSIS (IOFF, 1946)
EASTERN PALAEARCTIC—APODEMUS



54

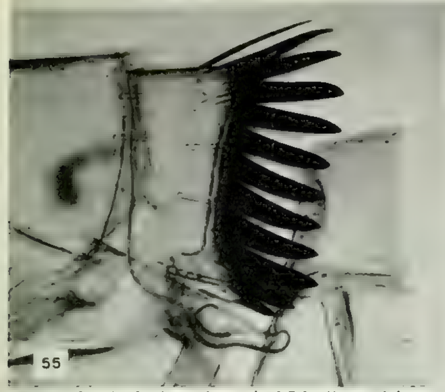
(IV.1)SIGMACTENUS ALTICOLA TRAUB, 1954
BORNEO—RATTUS (RATTUS)

PLATE 9

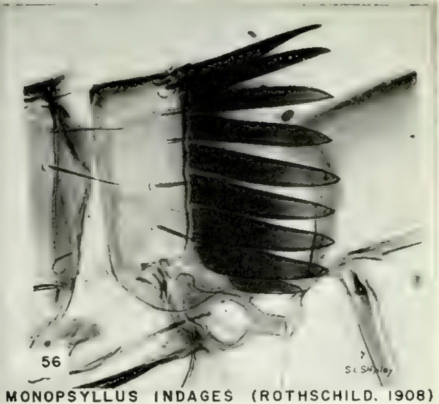
Pronotal Combs—**Monopsyllus** (iii.1)

FIG. 55 *Monopsyllus exilis* (Jordan, 1937) ex *Onychomys*—U.S.A.
FIG. 56 *Monopsyllus indages* (Rothschild, 1908) ex Squirrels and Chipmunks—Palaearctic
FIG. 57. *Monopsyllus thambus* (Jordan, 1929) ex *Peromyscus*—Nearctic (North)
FIG. 58 *Monopsyllus argus* (Rothschild, 1908) ex Flying-Squirrel—Palaearctic
FIG. 59. *Monopsyllus wagneri* (Baker, 1904) ex *Peromyscus*, etc.—North America
FIG. 60 *Monopsyllus sciurorum* (Schrank, 1803) ex Dormice—Palaearctic

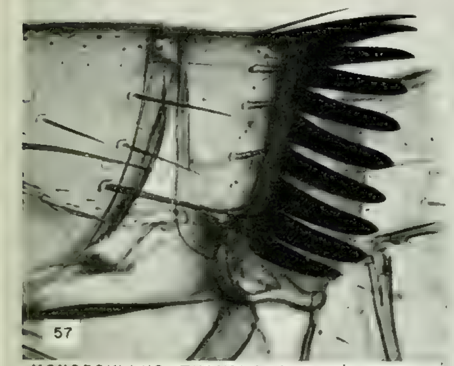
PRONOTAL COMBS — MONOPSYLLUS (III.1)



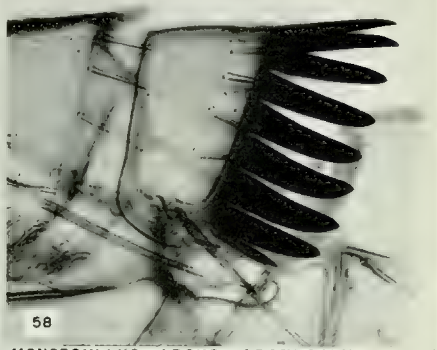
55 MONOPSYLLUS EXILIS (JORDAN, 1937)
EX. ONYCHOMYS – U.S.A.



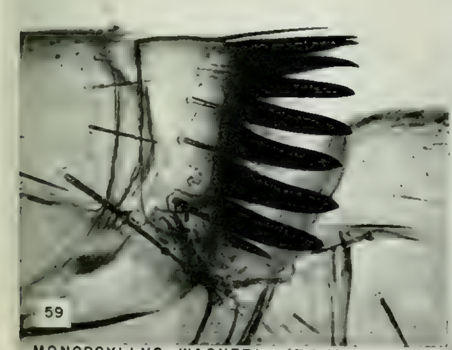
56 MONOPSYLLUS INDAGES (ROTHSCHILD, 1908)
EX. SQUIRRELS & CHIPMUNKS – PALAEARCTIC



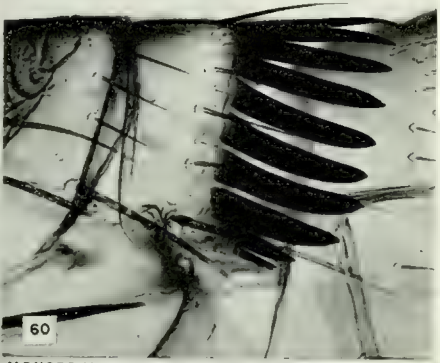
57 MONOPSYLLUS THAMBUS (JORDAN, 1929)
EX. PEROMYSCUS – NEARCTIC (NORTH)



58 MONOPSYLLUS ARGUS (ROTHSCHILD, 1908)
EX. FLYING-SQUIRREL – PALAEARCTIC



59 MONOPSYLLUS WAGNERI (BAKER, 1904)
EX. PEROMYSCUS, ETC. – NORTH AMERICA



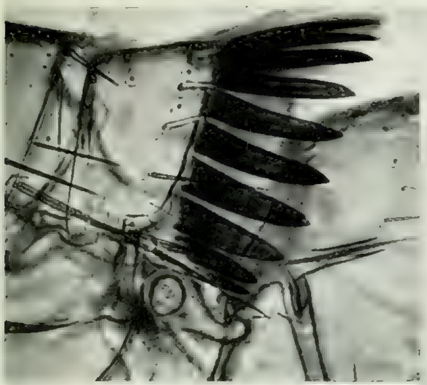
60 MONOPSYLLUS SCIURORUM (SCHRANK, 1803)
EX. DORMICE – PALAEARCTIC

PLATE 10

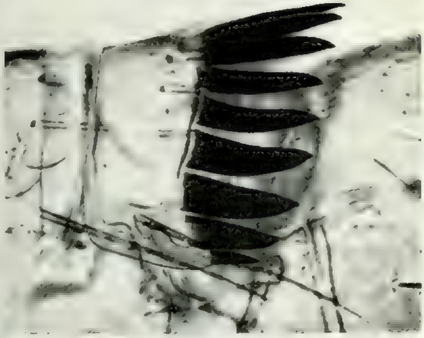
Pronotal Combs—**Monopsyllus** (iii.1)

Fig. 61 *Monopsyllus anisus* (Rothschild, 1907) Murids, etc.—Palaearctic
Fig. 62 *Monopsyllus ciliatus protinus* (Jordan, 1929) *Tamiasciurus*, *Eutamias*—Nearctic
Fig. 63 *Monopsyllus tolli* (Wagner, 1901) *Ochotona*—Holarctic
Fig. 64 *Monopsyllus vison* (Baker, 1904) *Tamiasciurus*—Nearctic
Fig. 65 *Monopsyllus eutamiadis* Augustson, 1941 Chipmunks—California
Fig. 66 *Monopsyllus fornacis* Jordan, 1937 Chipmunks—California

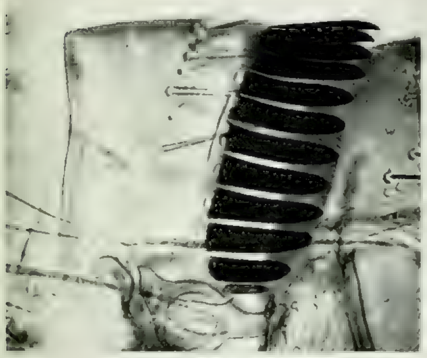
PRONOTAL COMBS—MONOPSYLLUS (III.1)



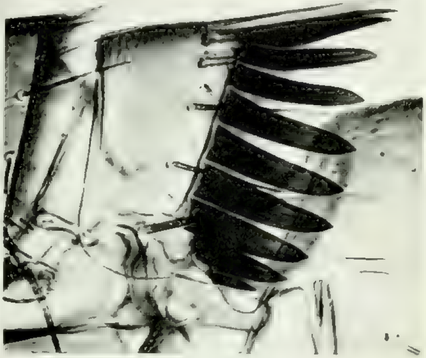
61 MONOPSYLLUS ANISUS (ROTHSCHILD, 1907)
PALAEARCTIC—MURIDS, ETC.



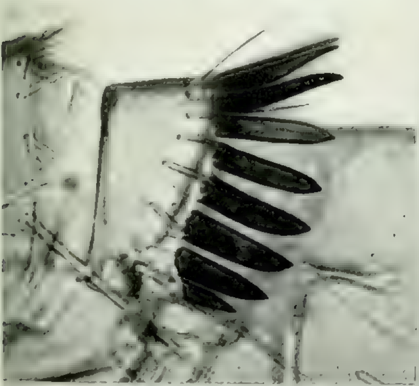
62 MONOPSYLLUS CILIATUS PROTINUS (JORDAN, 1929)
NEARCTIC—TAMIASCIURUS, EUTAMIAS



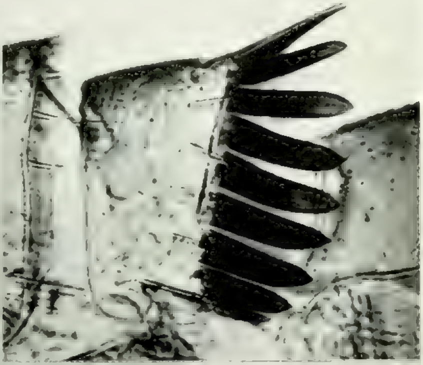
63 MONOPSYLLUS TOLLI (WAGNER, 1901)
HOLARCTIC—OCHOTONA



64 MONOPSYLLUS VISON (BAKER, 1904)
NEARCTIC—TAMIASCIURUS



65 MONOPSYLLUS EUTAMIADIS AUGUSTSON, 1941
CALIFORNIA—CHIPMUNKS



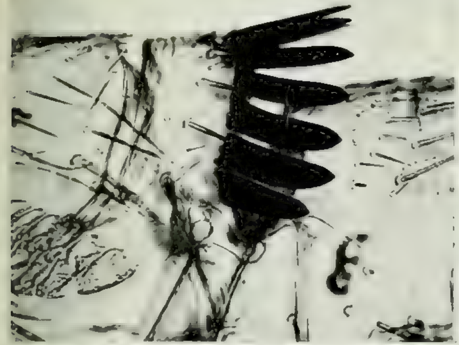
66 MONOPSYLLUS FORNACIS JORDAN, 1937
CALIFORNIA—CHIPMUNKS

PLATE 11

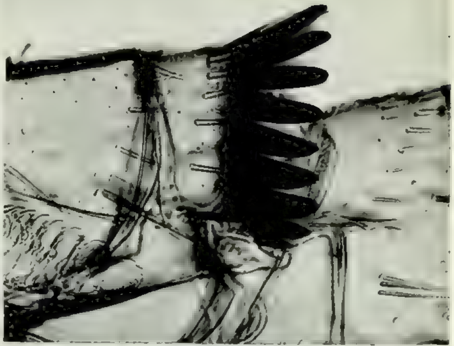
Pronotal Combs—Fleas of Underground Nests

FIG. 67. (i.7) *Catallagia charlottensis* (Baker, 1898) N. America—*Peromyscus*, etc.
FIG. 68. (iii.1) *Pleochaetis paramundus* Traub, 1950 Mexico—*Neotomodon*
FIG. 69. (i.7) *Epitedia cavernicola* Traub, 1957 U.S.A.—*Neotoma*
FIG. 70. (i.7) *Genoneopsylla thysanota* (Traub, 1968) Nepal—*Ochotona*
FIG. 71. (iv.2) *Caenopsylla laptevi* Mikulin & Zagniborodova, 1958 S.W. Asia—(Hosts?)
FIG. 72. (i.8) *Rhadinopsylla mexicana* (Barrera, 1952) Mexico—Peromyscines

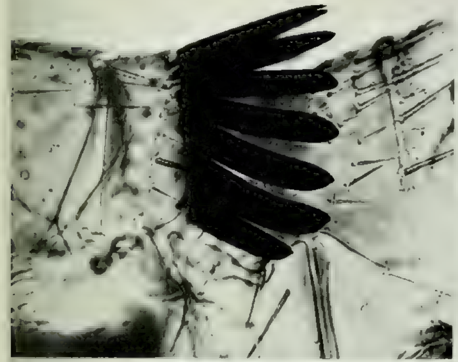
PRONOTAL COMBS- FLEAS OF UNDERGROUND NESTS



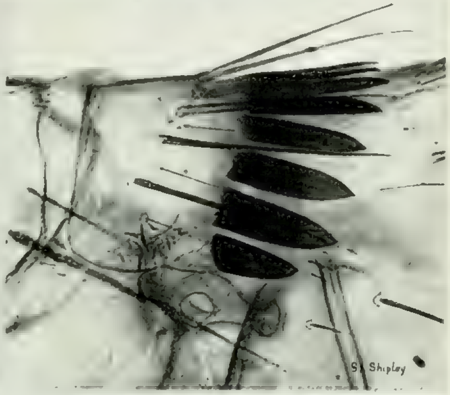
67 (I.7) CATALLAGIA CHARLOTTENSIS (BAKER, 1898)
N. AMERICA–PEROMYSCUS, ETC



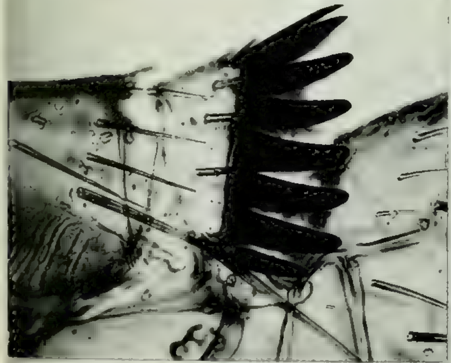
68 (III 1) PLEOCHAETIS PARAMUNDUS TRAUB, 1950
MEXICO – NEOTOMODON



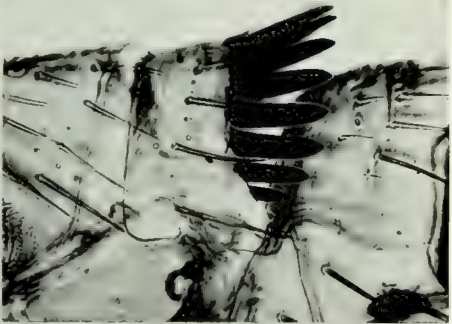
69 (I 7) EPITEDIA CAVERNICOLA TRAUB, 1957
U.S.A. — NEOTOMA



70 (I.7) GENONEOPSYLLA THYSANOTA (TRAUB, 1968)
NEPAL — OCHOTONA



71 (IV.2) CAENOPSYLLA LAPTEVI MIKULIN & ZAGNIBORODOVA, 1958 SW. ASIA-(HOST?)



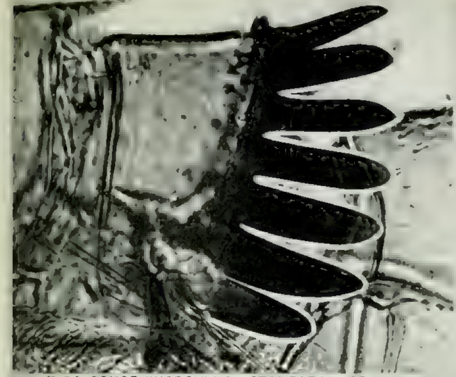
72 (I.8) RHADINOPSYLLA MEXICANA (BARRERA, 1952)
MEXICO-PEROMYSCINES

PLATE 12

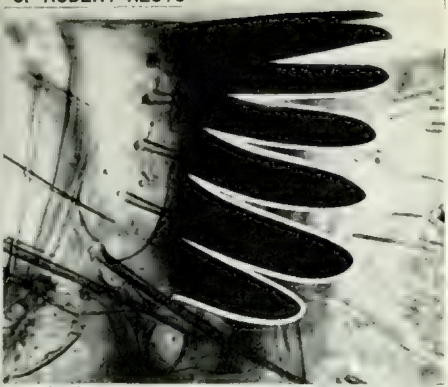
Pronotal Combs—Fleas of Rodent Nests

Fig. 73 (i.2) *Conorhinopsylla stanfordi* Stewart, 1930 Eastern U.S.A.—Squirrels
Fig. 74. (i.7) *Delotelis telegoni* (Rothschild, 1905) Western No. America—*Peromyscus*
Fig. 75 (i.2) *Megarthroglossus procus* J. & R., 1915 Western No. America—Squirrels
Fig. 76 (i.7) *Tamiophila grandis* (Rothschild, 1902) Eastern No. America—Chipmunks
Fig. 77 (i.7) *Epitedia faceta* (Rothschild, 1915) Eastern U.S.A.—Squirrels
Fig. 78. (i.7) *Phalacropsylla paradisea* Roths., 1915 So. Western U.S.—*Neotoma*

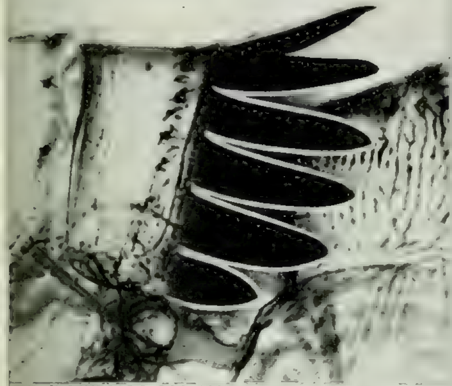
PRONOTAL COMBS — FLEAS OF RODENT NESTS



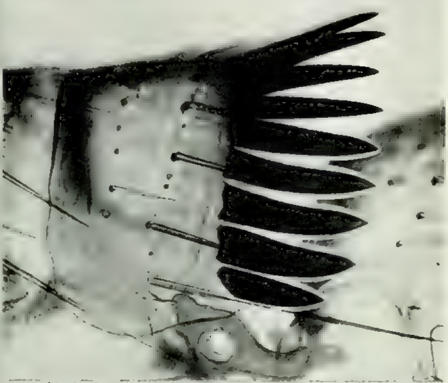
73 (I.2) CONORHINOPSYLLA STANFORDI STEWART, 1930
EASTERN U.S.A. – SQUIRRELS



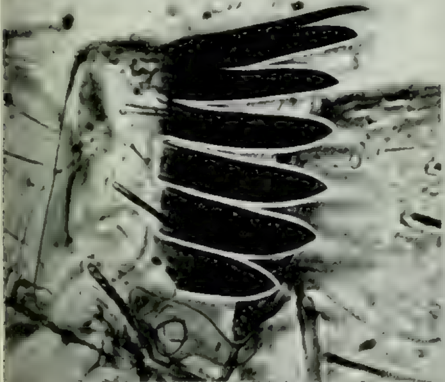
74 (I.7) DELOTELIS TELEGONI (ROTHSCHILD, 1905)
WESTERN NO. AMERICA – PEROMYSCUS



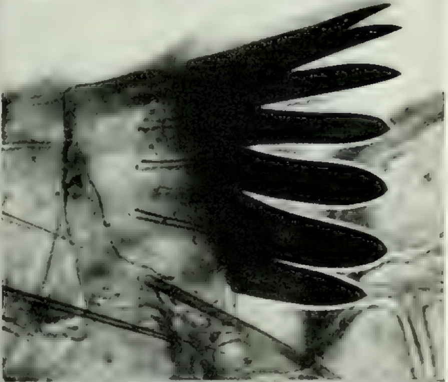
75 (I.2) MEGARTHROGLOSSUS PROCUS J. & R., 1915
WESTERN NO. AMERICA – SQUIRRELS



76 (I.7) TAMIOPHILA GRANDIS (ROTHSCHILD, 1902)
EASTERN NO. AMERICA – CHIPMUNK



77 (I.7) EPITEDIA FACETA (ROTHSCHILD, 1915)
EASTERN U.S.A. – SQUIRRELS



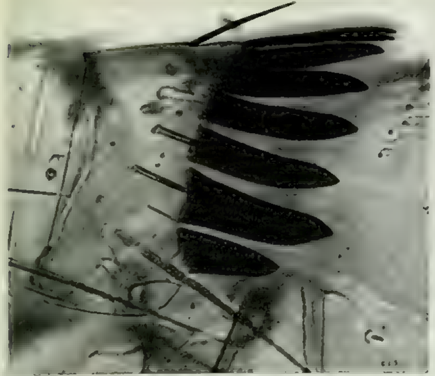
78 (I.7) PHALACROPSYLLA PARADISEA ROTHS., 1915
SO. WESTERN U.S. – NEOTOMA

PLATE 13

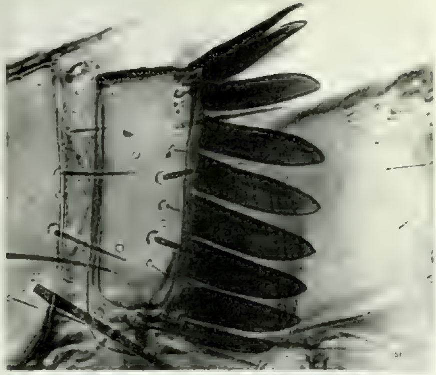
Pronotal Combs—Fleas of Underground Nests

Fig. 79. (i.7) *Strepsylla mina* Traub, 1950 Mexico—*Neotomodon*
Fig. 80. (iv.2) *Phaenopsylla kopetdag* Ioff, 1946 S.W. Asia—*Calomyscus*
Fig. 81. (i.7) *Catallagia striata* Scalon, 1950 E. Palaearctic—Voles
Fig. 82. (iv.2) *Paradoxopsyllus microphthalmus* Ioff, 1946 S.W. Asia—*Calomyscus*
Fig. 83. (i.2) *Wagnerina schelkovnikovi* Ioff & Argyropulo, 1934 S.W. Asia—*Meriones*
Fig. 84. (iii.1) *Callopsylla dolabris* (J. & R., 1911) S.E. Palaearctic—*Marmota*

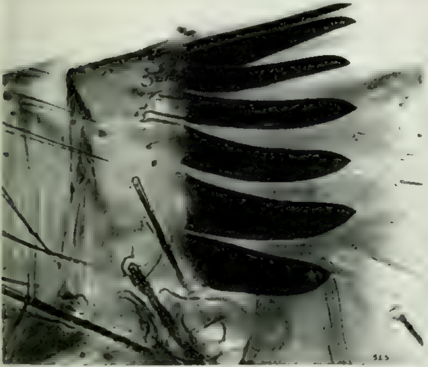
PRONOTAL COMBS—FLEAS OF UNDERGROUND NESTS



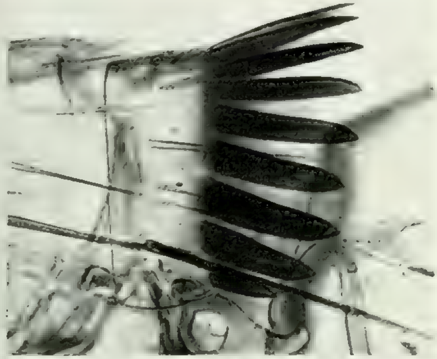
79 (I.7) STREPSYLLA MINA TRAUB, 1950
MEXICO—NEOTOMODON



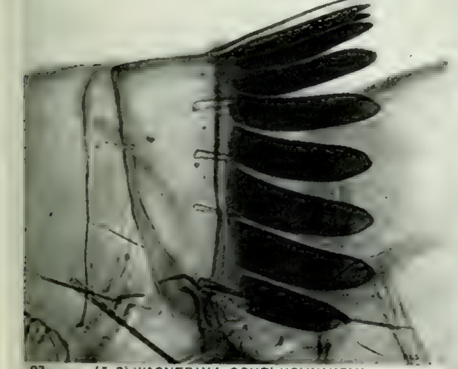
80 (IV 2) PHAENOPSYLLA KOPETDAG IOFF, 1946
SOUTH WESTERN ASIA—CALOMYSCUS



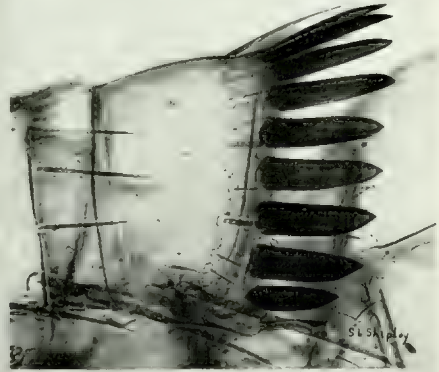
81 (I.7) CATALLAGIA STRIATA SCALON, 1950
EAST PALAEARCTIC—VOLES



82 (IV 2) PARADOXOPSYLLUS MICROPHTHALMUS
IOFF, 1946
SOUTH WESTERN ASIA—CALOMYSCUS



83 (I.2) WAGNERINA SCHELKOVNIKOVI
IOFF & ARGYROPULO, 1934
SOUTH WESTERN ASIA—MERIONES

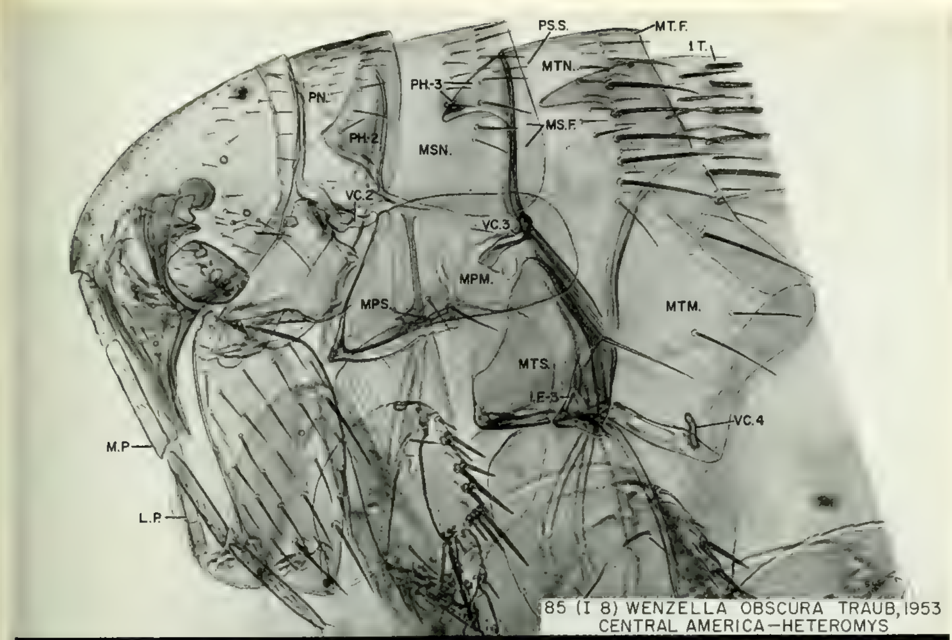


84 (III.1) CALLOPSYLLA DOLABRIS (J. & R., 1911)
SOUTH EASTERN PALAEARCTIC—MARMOTA

PLATE 14

Head and Thorax of Some Nest-Fleas

FIG. 85. (i.8) *Wenzella obscura* Traub, 1953 Central America—*Heteromys*
FIG. 86. (i.2) *Conorhinopsylla nidicola* Jellison, 1945 Nearctic—*Neotoma*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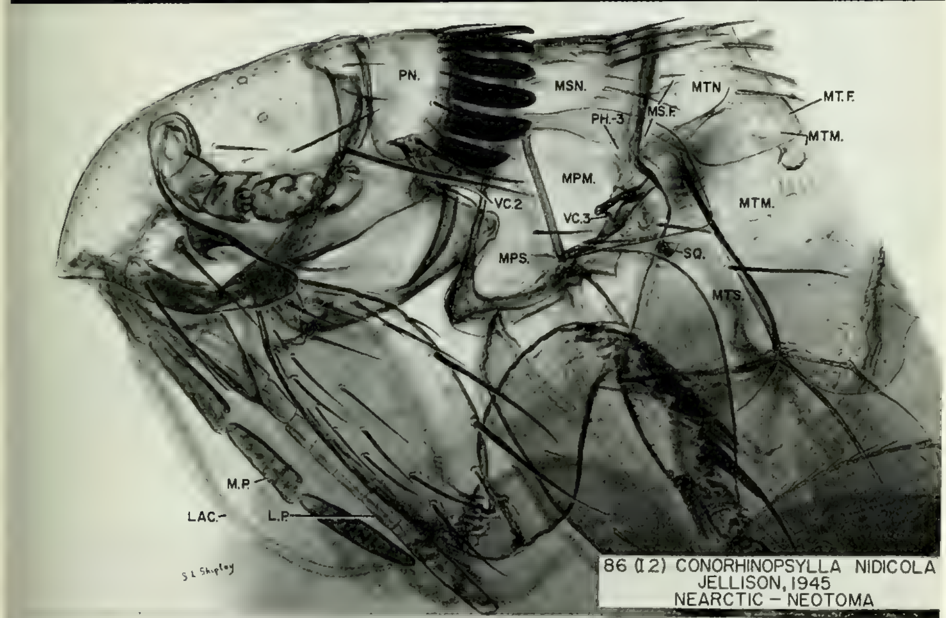
M.P
L.P.

85 (I 8) WENZELLA OBSCURA TRAUB, 1953
CENTRAL AMERICA—HETEROMYS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S L Shipley

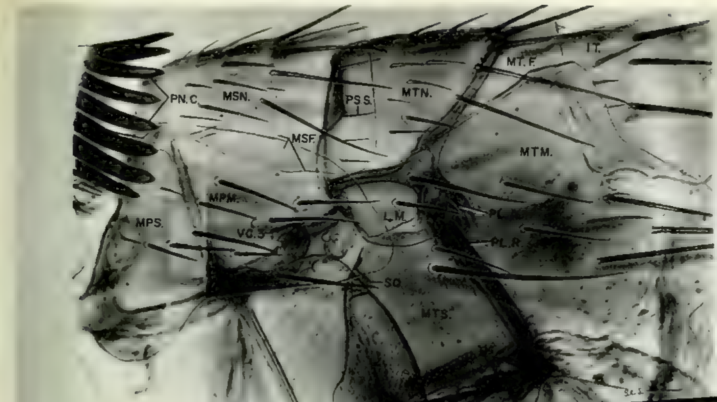
86 (I 2) CONORHINOPSYLLA NIDICOLA
JELLISON, 1945
NEARCTIC – NEOTOMA

HEAD AND THORAX OF SOME NEST-FLEAS

PLATE 15

Some Examples of the Thorax of Fleas

Fig. 87. (iii.1) *Opisodasys hollandi* Traub, 1947 Mexico—Tree-Squirrels
Fig. 88. (iii.1) *Opisodasys vesperalis* (Jordan, 1929) Nearctic—Flying-Squirrel
Fig. 89. (v.1) *Nycteridopsylla eusarca* (Dampf, 1908) Palaearctic—Bats



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PL.R.
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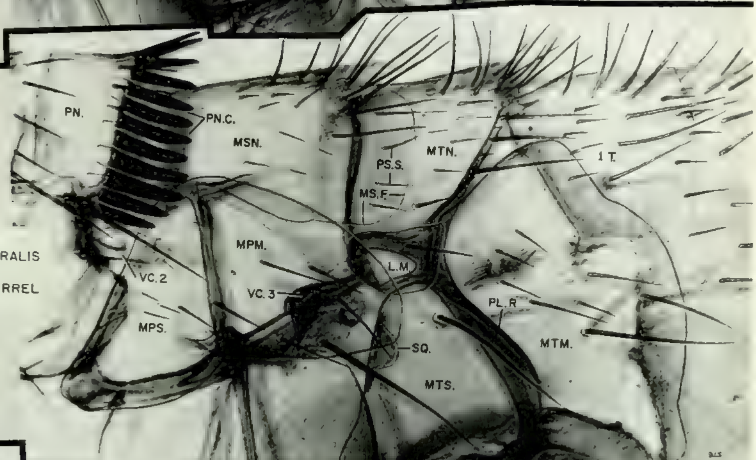
87
(III.1) OPISODASYS HOLLANDI
TRAUB, 1947
MEXICO—TREE-SQUIRREL



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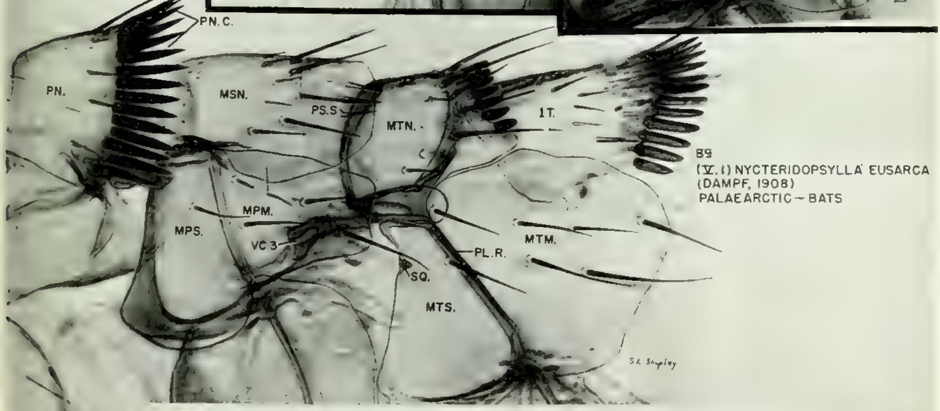
(III.1) OPISODASYS VESPERALIS
(JORDAN, 1929)
NEARCTIC—FLYING-SQUIRREL



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PL.R.
MTM.
SQ.
MTS.
S.L. Smyley

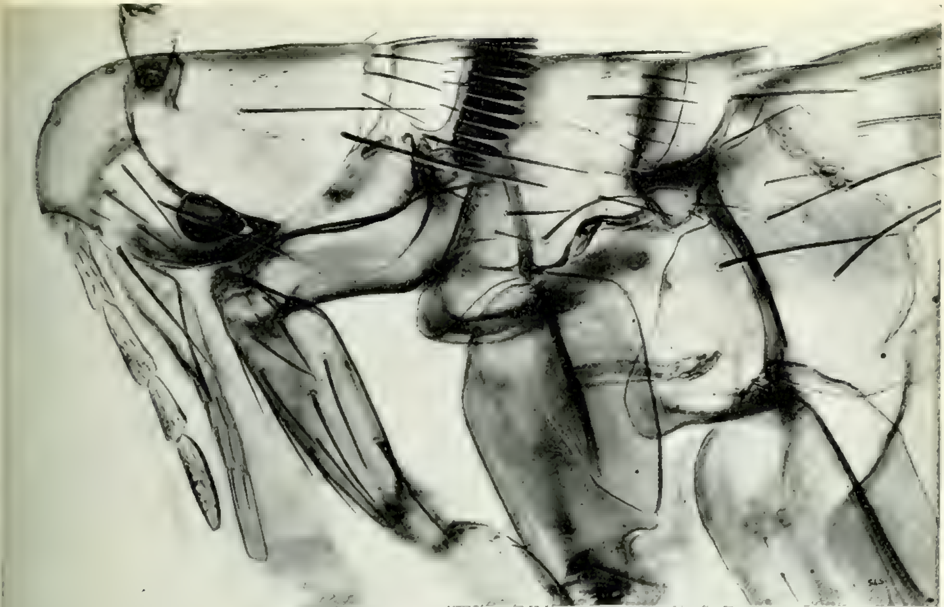
89
(V.1) NYCTERIDOPSYLLA EUSARCA
(DAMPF, 1908)
PALAEARCTIC—BATS

SOME EXAMPLES OF THE THORAX OF FLEAS

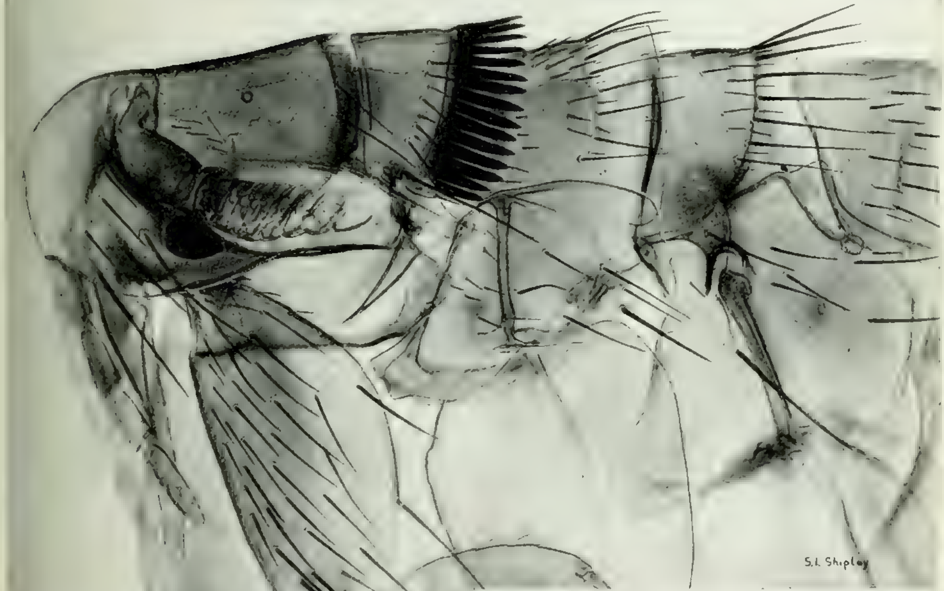
PLATE 16

Head and Thorax of Two **Ceratophyllus** From Cliff-Swallows

Fig. 90. (iii.1) *Ceratophyllus arcuegens* Holland, 1952 Palaearctic
Fig. 91. (iii.1) *Ceratophyllus styx* Rothschild, 1900 Palaearctic



90 (III. 1) CERATOPHYLLUS ARCUEGENS HOLLAND, 1952
NEARCTIC



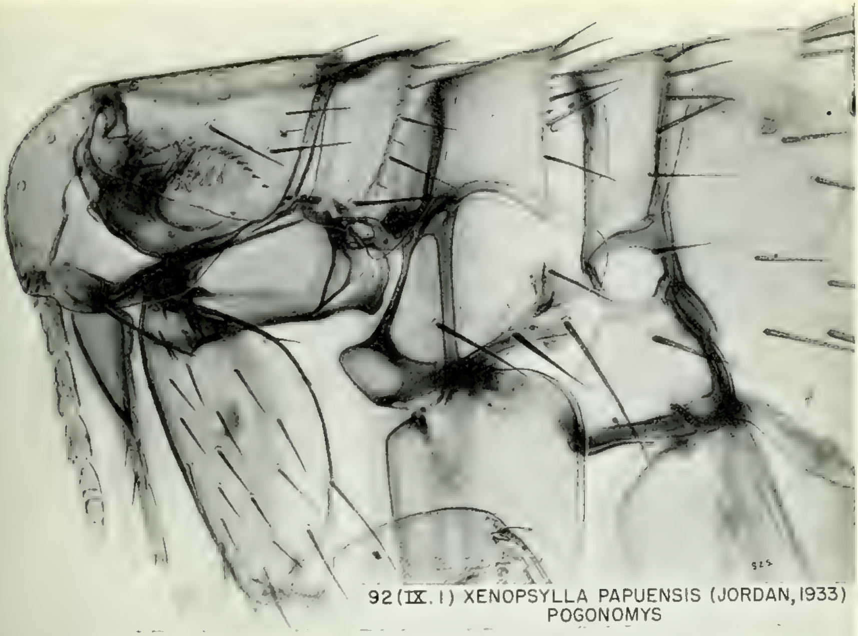
91 (III. 1) CERATOPHYLLUS STYX ROTHSCHILD, 1900
PALAEARCTIC

HEAD AND THORAX OF TWO CERATOPHYLLUS FROM CLIFF-SWALLOWS

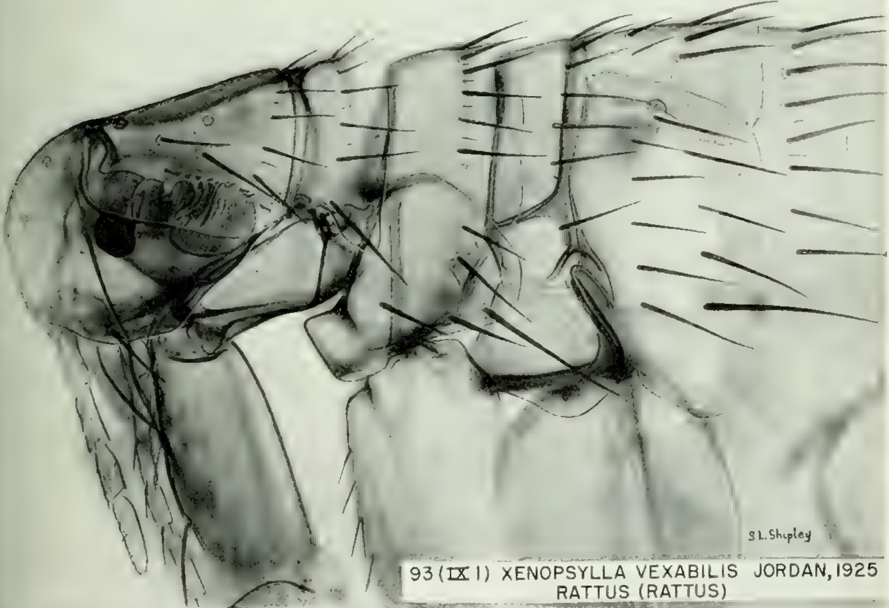
PLATE 17

Head and Thorax of Two **Xenopsylla** from New Guinea

Fig. 92. (ix.1) *Xenopsylla papuensis* (Jordan, 1933) *Pogonomys*
Fig. 93. (ix.1) *Xenopsylla vexabilis* Jordan, 1925 *Rattus* (*Rattus*)



92 (IX. 1) XENOPSYLLA PAPUENSIS (JORDAN, 1933)
POGONOMYS



93 (IX 1) XENOPSYLLA VEXABILIS JORDAN, 1925
RATTUS (RATTUS)

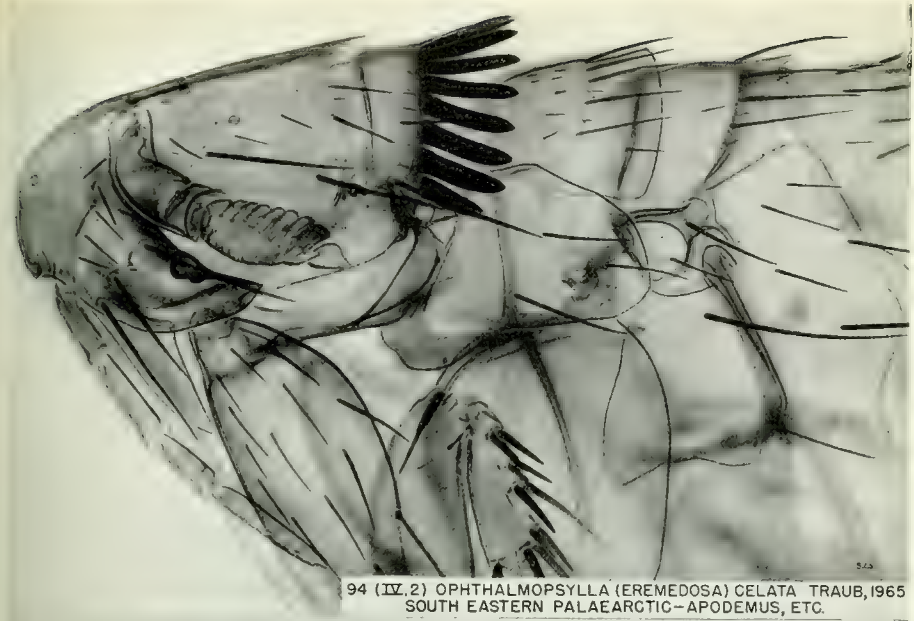
HEAD AND THORAX OF TWO XENOPSYLLA FROM NEW GUINEA

PLATE 18

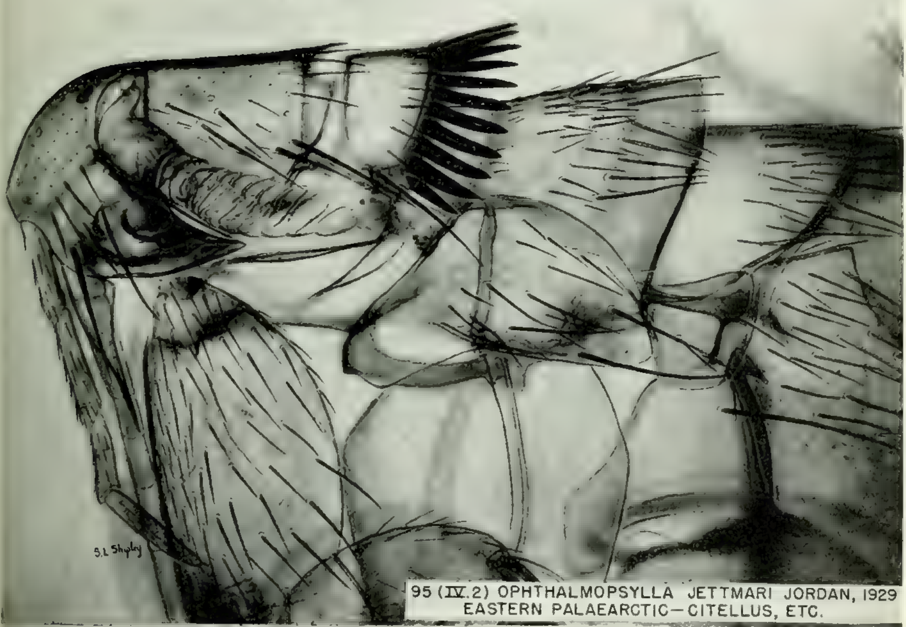
Head and Thorax of Two **Ophthalmopsylla**

FIG. 94. (iv.2) *Ophthalmopsylla* (*Eremedosa*) *celata* Traub, 1965 S.E. Palaearctic—*Apodemus*, etc.

FIG. 95. (iv.2) *Ophthalmopsylla jettmari* Jordan, 1929 E. Palaearctic—*Citellus*, etc.



94 (IV.2) OPHTHALMOPSYLLA (EREMEDOSA) CELATA TRAUB, 1965
SOUTH EASTERN PALAEARCTIC—APODEMUS, ETC.



95 (IV.2) OPHTHALMOPSYLLA JETTMARI JORDAN, 1929
EASTERN PALAEARCTIC—CITELLUS, ETC.

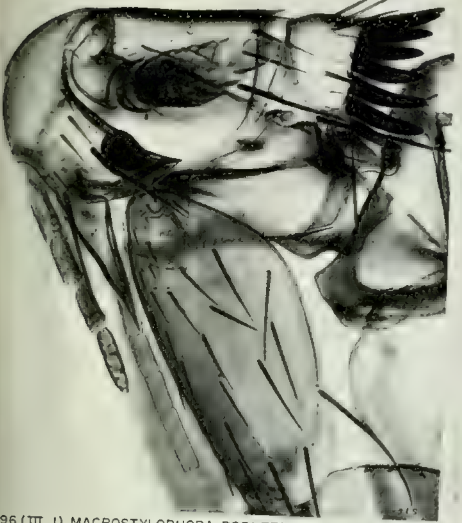
HEAD AND THORAX OF TWO OPHTHALMOPSYLLA

PLATE 10

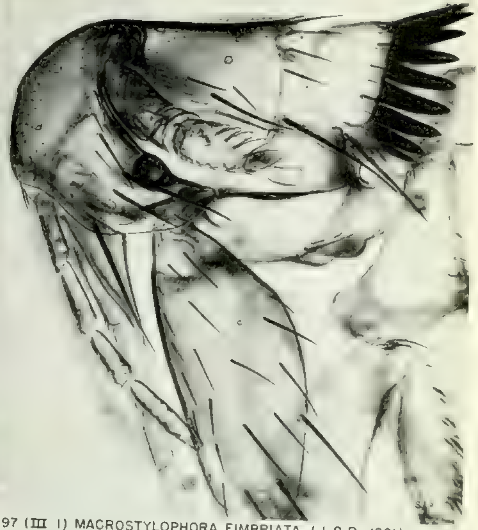
Contrasts in Head and Prothorax of Some Fleas

Fig. 96. (iii.1) *Macrostylophora borneensis* (Jordan, 1926) Borneo—Ground-Squirrels
Fig. 97. (iii.1) *Macrostylophora fimbriata* (J. & R., 1921) Himalayan—Flying-Squirrels
Fig. 98. (i.7) *Epitedia stanfordi* Traub, 1944 S.W. U.S.A.—*Peromyscus*
Fig. 99. (ix.1) *Actenopsyllus suavis* J. & R., 1923 California—Sea-Birds

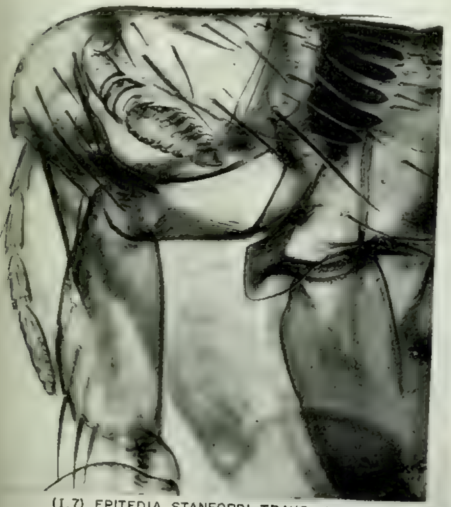
CONTRASTS IN HEAD AND PROTHORAX OF SOME FLEAS



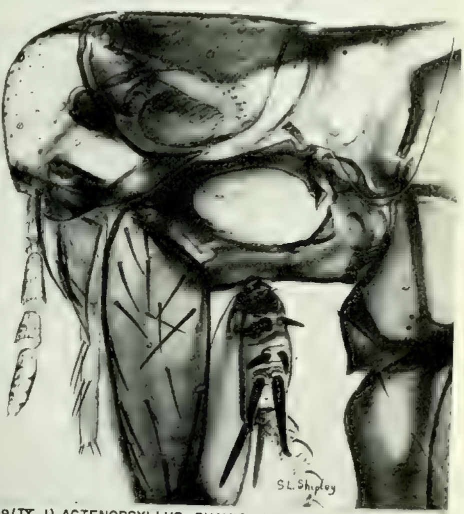
96 (III. 1) MACROSTYLOPHORA BORNEENSIS (JORDAN, 1926)
BORNEO–GROUND–SQUIRRELS



97 (III 1) MACROSTYLOPHORA FIMBRIATA (J. & R., 1921)
HIMALAYAN–FLYING–SQUIRRELS



98 (I. 7) EPITEDIA STANFORDI TRAUB, 1944
SOUTH WESTERN U.S.A.–PEROMYSCUS

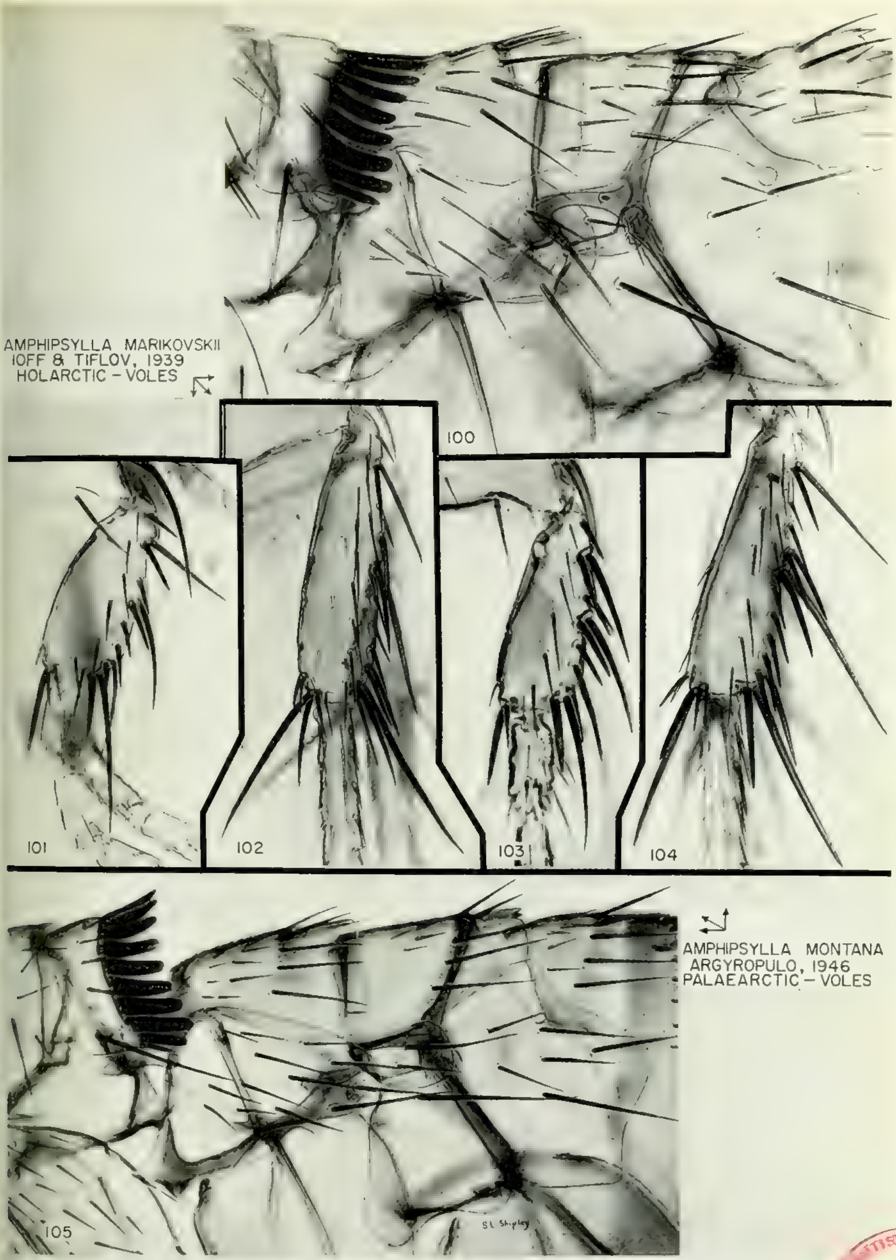


99 (IX. 1) ACTENOPSYLLUS SUAVIS J. & R., 1923
CALIFORNIA–SEA-BIRDS

PLATE 20

Thorax, Pro- and Metatibia of Two **Amphipsylla** (iv.2)

Fig. 100.	*Amphipsylla marikovskii* Ioff & Tiflov, 1939	Holarctic—Voles
Fig. 101.	*Amphipsylla marikovskii* Ioff & Tiflov, 1939	Holarctic—Voles
Fig. 102.	*Amphipsylla marikovskii* Ioff & Tiflov, 1939	Holarctic—Voles
Fig. 103.	*Amphipsylla montana* Argyropulo, 1946	Palaearctic—Voles
Fig. 104.	*Amphipsylla montana* Argyropulo, 1946	Palaearctic—Voles
Fig. 105.	*Amphipsylla montana* Argyropulo, 1946	Palaearctic—Voles


AMPHIPSYLLA MARIKOVSKII
IOFF & TIFLOV, 1939
HOLARCTIC – VOLES
100
101
102
103
104
AMPHIPSYLLA MONTANA
ARGYROPULO, 1946
PALAEARCTIC – VOLES
105
St Shipley

THORAX, PRO- & METATIBIA OF TWO AMPHIPSYLLA (IV.2)

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1967

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III ZOOGEOGRAPHY

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III ZOOGEOGRAPHY

BY

ROBERT TRAUB

Pp. 389-450

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III ZOOGEOGRAPHY

By ROBERT TRAUB

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SYNOPSIS

The Siphonapteran genus *Medwayella*, like other pygiopsyllids, is believed to have descended from fleas originating in the Australian Region, but it is a comparatively youthful taxon, with its centre of development in Borneo. Throughout its range, which is primarily in the Malayan Subregion, it is especially associated with callosciurine squirrels in the foothills and lower mountains. Other Oriental squirrel-fleas are of definite Palaearctic affinity, as are those of the insectivores and as is true for certain local murid-fleas. The data on Siphonaptera suggest that the squirrels and insectivores occurring in what is here termed the Insular Malayan Area, had their origin on the Asian Mainland. The route of entry to Borneo, however, seems to have been from Malaya through Sumatra or Java, rather than across the China Sea from Indo-China to northern Borneo. It is also clear that some members of the genus *Rattus*, and especially the subgenus *Rattus*, through the eons, must have moved back and forth between the Malayan Peninsula and Indonesia and Borneo, etc., since some of their fleas are of definite Palaearctic ancestry, and indeed one such genus occurs as far east as New Guinea. These rats, along with their fleas of Asian descent, are presumed to be recent entries, geologically speaking. However, the fleas of the more ancient rats in New Guinea and the so-called 'Maltilindo Archipelagoes' are all pygiopsyllids and are believed to have had their roots in the Australian Region, and the forebears of these murids themselves may have originated there as well.

Malaya, Sumatra, Java and Borneo share many faunal features, although the Javanese fauna is relatively impoverished, while the mammals and fleas of Sarawak resemble those of Malaya more closely than do those of Sabah. Palawan seems to have obtained its squirrels and tree-shrews and some rats and related fleas from northeast Borneo, while much of the Mindanao fauna apparently entered from southeastern Sabah. Mindanao, however, also has faunal elements from Celebes and the New Guinean Subregion. The data also provide support for the theory of Continental Drift in suggesting that there were ancient faunal connections, involving 'island-hopping' mammals and their fleas, between the Southern Continents.

I. INTRODUCTION

STUDY of the distribution and hosts of the genera of Siphonaptera treated in the first article in this series not only contributes to our understanding of the zoogeography of fleas and of their hosts, particularly as pertains to Southeast Asia and the islands of the Oriental Region, but also appears to be of significance in subjects as far afield as the theory of Continental Drift (Traub, in prep.) and medical geography (Traub et al., in prep.). Accordingly, an analysis of the geographic and host relations is herewith presented in some detail, along lines listed in the Table of Contents, and the data suggest that the forebears of *Medwayella* Traub, 1972, and other pygiopsyllids originated in the Australian Region or Wallacea, not the Asian mainland, but that other Oriental squirrel-fleas (and the squirrels) and the non-pygiopsyllid fleas of the subgenus *Rattus* Fischer, 1803, were derived from Palaearctic stocks. The data also indicate that Java has had a different faunal history than has Sumatra, and that the rodents and fleas of Sarawak have significantly more in common with Malaya than do those of North Borneo (Sabah). Evidence suggesting that there were tenuous, aboriginal faunal connections between the southern continents, as by 'island-hopping' mammals, is mentioned only briefly and occasionally, since the subject of Continental Drift will be treated in detail elsewhere (Traub, in prep.).

In order to facilitate the discussion, much of the basic data and observations on pertinent Siphonaptera and their hosts are presented first, in a special section which includes a review of squirrel-fleas from various parts of the world. Generalizations and deductions based upon such material are presented in the subsequent section on Discussion, where highlights of the data are reviewed, and where new information (citing sources) is given as required. The section on Conclusions summarizes the results.

In general, the Zoogeographic Regions and Subregions cited here are those used by Bartholomew, Clarke & Grimshaw (1911), but with certain new qualifications regarding Subregions, based upon unpublished notes (Traub & Hoogstraal, in litt.). Thus, it has been recognized that a map-reading alone is insufficient for denoting the limits of a Subregion, since the ecology of a particular area, depending upon the altitude or rainfall, may be an over-riding factor. Hopkins & Rothschild (1966) therefore refer to 'the occurrence of "islands" which belong faunistically to one region in a "sea" of another' and cite, as an example, the fact that the mountains of Guatemala and southern Mexico evidently have a Nearctic flea-fauna though that of the lowlands at their foot is Neotropical. In the present article, this concept has been extended. Thus, the *mesic* elements of the Himalayas and adjacent mountains, and the mountains of Formosa (Taiwan) are deemed as being in the 'Eastern Palaearctic Subregion'. Instead of being placed in the Oriental Region as heretofore, the *xeric* parts of western Pakistan and India, etc., are here considered as being in the 'Southeastern Palaearctic Subregion' (along with the arid side of the Himalayas), since their faunal affinities are with the deserts of Soviet Central Asia and Iran. The Oriental Region is herein divided into the following Subregions: (1) The Indian Subregion, as used in this paper, is limited to the plains and monsoon areas of the subcontinent, western Burma, Ceylon, the terai of Nepal, etc. (2) What is here termed the 'Burmo-Chinese Subregion' encompasses not only the continent from Assam east to Indo-China, but south to northern Malaya, and including the foothills and lowlands of Formosa. (3) The 'Malayan Subregion' as used here includes Malaya south of Perlis, Borneo, Sumatra, Java, Bali and Palawan (Philippines). The other islands of the Philippines are a zoogeographic problem and have been assigned to various Subregions (Darlington, 1963) or ignored. Tentatively, I am placing Luzon in the Southeastern Oriental Subregion, and the remaining islands in the Malayan Subregion. Unpublished data suggest that Mindanao has some faunal similarities with Celebes, which is here placed in the 'Wallacean Subregion' (Wallacean Region) along with Timor and the Lesser Sundas. It is impossible for me to evaluate such observations without adequate information about the Siphonaptera and mammals of the lowlands, foothills and mountains of Mindanao and of Celebes. The Moluccas, Ceram, etc., are placed in the Moluccan Subregion, but we have no data on Siphonaptera from those islands.

In accordance with this concept of using ecological factors and faunal affinities in denoting zoogeographical areas, the Nearctic Region is regarded as extending along the upper regions of the mountain ranges into northern South America. These montane areas commencing south of the deserts of northern Mexico are termed the 'Temperate Middle American Subregion', while the Neotropical Region is viewed as extending north along the coasts of Mexico.

From the geographic or cartographic point of view this system has drawbacks. Thus, it is awkward to have the Oriental Region rent by the vast mountain-ranges of the Himalayan Chain, so that, for example, much of Burma and south Yunnan are both in the Oriental Region, but between them are massive Palaearctic 'islands' of the Himalayas. However, faunistically and geologically, this makes sense. The Himalayas are actually a young group of mountains, and it appears that the tremendous ecological changes wrought by the relatively recent upthrusts (e.g. creation of deserts in the rain-shadows) have obliterated or drastically modified florae and faunae that formerly were distributed continuously across much of southern Asia. As a result, despite the extensive patches of desert, there exist 'ecological islands' scattered amongst the mountains throughout the region, where these same groups of mammals, ectoparasites, associated microbial infections and plant-habitats may be found as relics of past eons (Traub & Evans, 1967; Traub & Wisseman, 1968).

Allusion was made, in the first article in this series, to the difficulties posed by the multiple meanings ascribed to geographical names, especially when the terms acquire political connotations which vary with the passage of time. Good (1964), for example, referred to the confusion associated with the name Malaya and its allied forms, and therefore defined and limited such usage in his opus (p. 20) as follows: (1) Malay Peninsula—'that part of continental Asia south of the isthmus of Kra'; (2) Malayan Archipelago—'the islands thence as far as and including New Guinea' and (3) Malaysia—'both together'. This is a useful terminology, but the current use of the name Malaysia to denote the countries of Malaya and the former British colonies in Borneo has added a new source of confusion. Also, in zoogeography, apparently in contrast to plant-geography, it is desirable to deal with New Guinea and adjacent islands as an entity rather than something submerged in a 'Malayan Archipelago'. A different terminology is required, and valid objections can be, and have been, raised to all proposals. Nevertheless, for purposes of convenience, utility and uniformity, it seems desirable to select and specify names for the main geographic areas used in this paper. Accordingly, in addition to the

Regions and Subregions as defined above, and the standard names of countries and islands, etc., the following are employed: (1) 'Malayan Peninsula' for the continental area south of the Isthmus of Kra. (2) The acronym 'Malfilindo Archipelagoes' for the entire groups of islands of Indonesia, Philippines and Borneo but excluding the islands of the New Guinean Subregion. (3) 'Southeast Asian Mainland' for the entire continental land-mass encompassed in the Oriental Region with the exclusion of the Indian Subregion. The Palaearctic portions of the Himalayas are therefore included. (4) The 'Oriental Mainland of Southeast Asia' refers to that same area in the zoogeographic sense, i.e. limited purely to the Oriental aspects and therefore excluding the Himalayas. (5) 'Insular Malayan Area' for the islands of the Malayan Subregion, i.e. Borneo, Java, Sumatra and the Philippines (excluding Luzon). (6) Australo-Asian Archipelagoes for the entire group of islands, from Sumatra and the Philippines to, and including, New Guinea and Australia.

Two other points are mentioned for clarification and emphasis. Throughout, the term 'Oriental' has a zoogeographic connotation, meaning the Oriental Region, and it is *not* used in the geographic, political, ethnological or popular sense denoting China and Japan. Secondly, unless otherwise indicated, all comments about numbers of taxa of Siphonaptera refer to the fleas of non-volant hosts only, and not necessarily to all the known genera or species. This approach is desirable in zoogeography because bats and birds may fly enormous distances, and the fleas found on them in one area may really be more representative of another, having accompanied the host on its journey.

The sources for the scheme of taxonomy and nomenclature of mammals are presented near the end of the article (p. 443), but scientific references are cited when unusual or controversial names are used.

The data presented below, in essence, include all the known fleas from Malaya, Sarawak, Sabah, Thailand, Indo-China, the Philippines, etc., with the exception of commensal species, bat-fleas and bird-fleas.

II. DATA AND OBSERVATIONS

A. Distribution of Relevant Mammals in Pertinent Areas

1. Introduction

In discussing the zoogeography of fleas, it is necessary to consider that of the hosts, and accordingly data are first presented on the distribution of the major hosts for which we have records on mammal-fleas, in the Burmo-Chinese and Malayan Subregions of the Oriental Region. Data on Siphonaptera will be presented thereafter.

It should be borne in mind that no effort is made to treat all the rats and squirrels that occur within the geographical areas cited, since in some important instances data on Siphonaptera are lacking. Even with these limitations, however, certain generalizations appear warranted and zoogeographic trends can be noted which appear valid, as will be shown later.

Members of the sciurid tribe Callosciurini of the subfamily Sciurinae are particularly well represented in the Malayan and Burmo-Chinese Subregions, and since these tree-squirrels and 'ground-squirrels' have a relatively rich Siphonapteran fauna, and apparently constitute the main hosts of the genus *Medwayella*, they are treated in some detail. The Petauristinae, or flying-squirrels, are also wealthy in numbers of genera and species in this Subregion, certainly far more so than in the Palaearctic and Nearctic Regions. However, since relatively little is yet known about the fleas of Oriental flying-squirrels, these mammals are not included in the charts listing geographic areas, and are mentioned only briefly throughout.

2. Squirrels and Murids Occurring in Malaya and Borneo

Malaya and Borneo have a rich fauna of murids and squirrels, especially callosciurines, both as genera and as species, as indicated in Table 1. It is noteworthy that a significant number of the genera, and even the species, are found in both areas. Thus, Malaya and Borneo share 6 of 12 genera of squirrels and 3 of 7 murids, while 9 out of 25 species of squirrels, and 12 of 30 non-commensal species of murids are found in both areas. Further, some of the species treated as distinctive are actually closely allied, so that, for example, the Malayan *Rattus* (*Stenomys*) *bowersi* (Anderson, 1879) may be regarded as a sibling species of the Bornean *R.* (*S.*) *infraluteus* (Thomas, 1888) (just as their respective fleas are siblings), and the Malayan *R.* (*Lenothrix*) *inas* Bonhote, 1906, deemed the twin species of Bornean *R.* (*L.*) *alticola* (Thomas, 1888). However, it is also pointed out that Borneo exhibits an important degree of endemicity, especially with respect to sciurids. Thus, *Rheithrosciurus* Gray, 1867, and *Glyphotes* Thomas, 1898, are found nowhere else, while *Exilisciurus* Moore, 1958, is known elsewhere only from the Philippines, and *Nannosciurus* Trouessart, 1880, from Java and Sumatra. *Haeromys* Thomas, 1911, occurs only in Celebes and Borneo. The Malayan taxa not listed for Borneo are generally northern forms reaching the limit of their ranges in Malaya (e.g. *Hapalomys* Blyth, 1859, *Bandicota* Gray, 1873, and *Menetes* Thomas, 1908), or else are restricted to Malaya, Sumatra and Java, such as *Pithecheir* Cuvier, 1838.

Of particular relevance is the distribution of non-commensal murids and squirrels within Borneo, especially insofar as concerns Malayan species, and this is treated in Table 2. (Since little is known about the fleas of Indonesian Borneo or Brunei, those regions are not considered herein.) Of the mammals listed, 10 of the murids and 7 of the squirrels are found in all 3 areas. Six of the rats and 9 of the squirrels are absent from Malaya. Three of the rodents are limited to Malaya and Sarawak, viz., *Rattus* (*Lenothrix*) *canus* (Miller, 1903), *Lariscus* (*L.*) *insignis* (F. Cuvier, 1821) and *Sundasciurus* (*S.*) *tenuis* (Horsfield, 1824). Of the Bornean rats, 3 are found only in North Borneo (Sabah), and there is 1 species of squirrel which is known only from Sarawak. *Glyphotes* (*G.*) *simus* Thomas, 1898 and *Lariscus* (*Paralariscus*) *hosei* (Thomas, 1892) are reported only from northern Sarawak and from Sabah, while *Rheithrosciurus macrotus* (Gray, 1856) apparently does not occur farther north than the south of Sabah.

It therefore appears that there are rather significant faunal differences between Sabah and Sarawak, even though a large proportion of these rodents occur in both areas, and even Malaya as well. It is noteworthy that none of the rodents common to both Sabah and Malaya are absent from Sarawak, suggesting that the path of migration was via Sarawak.

Table I

Species of squirrels (excluding flying-squirrels) and murids occuring in Malaya and Borneo

Murids	Malaya	Borneo
Bandicota bengalensis	+	
Bandicota indica	+	
Chiropodomys gliroides	+	+
Chiropodomys major		+
Chiropodomys muroides		+
Haeromys margarettae		+
Haeromys pusillus		+
Hapalomys longicaudatus	+	
Mus musculus	+	+
Pithecheir melanurus	+	
Rattus (*Leno.*) *alticola*		+
Rattus (*Leno.*) *baeodon*		+
Rattus (*Leno.*) *canus*	+	+
Rattus (*Leno.*) *inas*	+	
Rattus (*Leno.*) *ochraceiventer*		+
Rattus (*Leno.*) *rajah*	+	+
Rattus (*Leno.*) *surifer*	+	+
Rattus (*Leno.*) *whiteheadi*	+	+
Rattus (*Leop.*) *edwardsi*	+	
Rattus (*Leop.*) *sabanus*	+	+
Rattus (*Maxomys*) *cremoriventer*	+	+
Rattus (*Maxomys*) *fulvescens*	+	+
Rattus (*Maxomys*) *niviventer*	+	
Rattus (*Rattus*) *annandalei*	+	
Rattus (*Rattus*) *argentiventer*	+	+
Rattus (*Rattus*) *baluensis*		+
Rattus (*Rattus*) *exulans*	+	+
Rattus (*Rattus*) *norvegicus*	+	+
Rattus (*Rattus*) *rattus*	+	+
Rattus (*Rattus*) *tiomanicus*	+	+
Rattus (*Stenomys*) *bowersi*	+	
Rattus (*Stenomys*) *infraluteus*		+
Rattus (*Stenomys*) *muelleri*	+	+

Squirrels	Malaya	Borneo
Callosciurus albescens		+
Callosciurus caniceps	+	
Callosciurus erythraeus	+	
Callosciurus nigrovittatus	+	+
Callosciurus notatus	+	+
Callosciurus prevosti	+	+
Dremomys everetti		+
Dremomys rufigenis	+	
Exilisciurus exilis		+
Exilisciurus whiteheadi		+
Glyphotes (*G.*) *simus*		+
Glyphotes (*Hess.*) *canalvus*		+
Lariscus (*L.*) *insignis*	+	+
Lariscus (*Para.*) *hosei*		+
Menetes berdmorei	+	
Nannosciurus melanotis		+
Ratufa affinis	+	+
Rheithrosciurus macrotis		+
Rhinosciurus laticaudatus	+	+
Sundasciurus (*Alte.*) *hippurus*	+	+
Sundasciurus (*S.*) *brookei*		+
Sundasciurus (*S.*) *jentinki*		+
Sundasciurus (*S.*) *lowi*	+	+
Sundasciurus (*S.*) *tenuis*	+	+
Tamiops macclellandi	+	

Summary—Numbers of taxa

I. Genera	Squirrels	Murids
Total	12	7
Number in common	6	3
Absent from Malaya	4	1
Absent from Borneo	2	3

II. Species	Squirrels	Murids
Total	25	33
Number commensal	0	3
No. of others in common	9	12
Absent from Malaya	11	9
Absent from Borneo	5	9

TABLE 2

Occurrence in Sarawak, Sabah and Malaya of certain squirrels and murids

Murids	Malaya	Sarawak	Sabah
Chiropodomys gliroides	+	+	+
Haeromys margarettae		+	+
Rattus (*Leno.*) *alticola*			+
Rattus (*Leno.*) *baeodon*		+ (North)	
Rattus (*Leno.*) *canus*	+	+	
Rattus (*Leno.*) *ochraceiventer*		+	+
Rattus (*Leno.*) *rajah*	+	+	+
Rattus (*Leno.*) *surifer*	+	+	+
Rattus (*Leno.*) *whiteheadi*	+	+	+
Rattus (*Leop.*) *sabanus*	+	+	+
Rattus (*Maxomys*) *cremoriventer*	+	+	+
Rattus (*Maxomys*) *fulvescens*	+	+	+
Rattus (*Rattus*) *argentiventer*	+	+	+
Rattus (*Rattus*) *baluensis*			+
Rattus (*Rattus*) *tiomanicus*	+	+	+
Rattus (*Stenomys*) *infraluteus*			+
Rattus (*Stenomys*) *muelleri*	+	+	+

Squirrels	Malaya	Sarawak	Sabah
Callosciurus albescens		+	+
Callosciurus nigrovittatus	+	+	+
Callosciurus notatus	+	+	+
Callosciurus prevosti	+	+	+
Dremomys everetti		+	+
Exilisciurus (2 species)		+	+
Glyphotes (*G.*) *simus*		+ (North)	+
Glyphotes (*Hess.*) *canalvus*		+	
Lariscus (*L.*) *insignis*	+	+	
Lariscus (*Para.*) *hosei*		+ (North)	+
Nannosciurus melanotis		+	
Ratufa affinis	+	+	+
Rheithrosciurus macrotis		+	+ (South)
Rhinosciurus laticaudatus	+	+	+
Sundasciurus (*Alte.*) *hippurus*	+	+	+
Sundasciurus (*S.*) *brookei*		+	+
Sundasciurus (*S.*) *jentinki*		+	+
Sundasciurus (*S.*) *lowi*	+	+	+
Sundasciurus (*S.*) *tenuis*	+	+	

3. Tree-Shrews (Tupaiidae)

The group of mammals whose over-all distribution corresponds most closely to that of fleas of the genus *Medwayella* is that of the tupaiids, and hence these merit discussion. The classification of tupaiids is in rather confused state at both the ordinal level and that of the species. The tree-shrews are regarded as menotyphlous insectivores by Anderson & Jones (1967) but as lemuroid primates by Simpson (1945), Walker et al. (1968) and Morris (1965). The family was reviewed by Lyon (1913), but many of his 'species' are no longer recognized as such, if at all, and there has been no subsequent single work dealing with the distribution of tupaiids. Instead, mammalogists working with certain geographical areas have at times cited the relevant species, and even here a variety of names have been used for a single species. Table 3 lists the species of tupaiids occurring in specified regions, and presumably the only member of the family not cited is *Tupaia nicobaria* (Zelebor, 1869), of the Nicobar Islands. In compiling the list, Ellerman & Morrison-Scott (1951) was used as the authority for the range of *T. glis* (Diard, 1820) and *T. minor* Günther, 1876; Morris (1965) for tupaiids from Sumatra and Java; Medway (1963) for Borneo; Harrison (1964) for Malaya, and Taylor (1934) for *Urogale* Mearns, 1905.

It is apparent that the contemporary range of the family is wholly in the Oriental Region, from India to Palawan and Mindanao in the Philippines. Only 1 species, of a distinctive endemic genus, occurs in India and only 1 species (*Dendrogale murina* (Schlegel & Müller, 1845)) is found in Indo-China, while the second species of *Dendrogale* Gray, 1848, is restricted to Borneo. The monotypic *Urogale* is endemic to the Philippines (Mindanao). *Tupaia* Raffles, 1821, has the broadest range and the largest number of species, and its height of development seems to have been in Borneo, with 8 species listed for Sarawak and 5 of these occurring in North Borneo. Two of the Bornean species, *T. glis* and *T. minor*, occur in Malaya, and the former ranges from Assam to Palawan. It is of interest that 2 tupaiids (the monotypic *Ptilocercus* Gray, 1848, and *T. minor*) which are found in Sumatra, Malaya and Borneo, are absent from Java.

4. Additional Data on Mammals

Some of the tables which deal with the distribution of Siphonaptera, viz., Tables 6 and 7, also present data on relevant mammalian hosts, particularly insofar as concerns other areas of the Oriental Region. Thus, squirrels are treated in Table 6 (facing p. 404), whence it can be seen that certain species, such as *Tamiops macclellandi* (Horsfield, 1839) and *Menetes berdmorei* (Blyth, 1849), have a more northern or continental type of distribution, being found in Indo-China, Thailand and Malaya, but not Indonesia or Borneo, etc. *Callosciurus caniceps* Gray, 1842, is also in this category, but it occurs in Formosa (Taiwan) as well. The genus *Dremomys* Heude, 1898, as a whole, is wide-ranging in the Region, extending beyond some of the extremes of the Table, since it is also present in Nepal, south China, Assam, Burma and even Formosa. It is not known from the Philippines.

Most of the pertinent species of *Callosciurus* Gray, 1867, have a rather southern and eastern distribution—Malaya, Indonesia and Borneo, with *C. prevosti* Desmarest, 1822, and *C. notatus* Boddaert, 1785, reaching Celebes, and members of the

TABLE 3

Distribution of genera and species of tupaiids (primates, Tupaiidae) in specified areas

Genus and total number of species	South India	Assam or Burma	South China	Thailand	Indo-China	Malaya	Sumatra	Java	Borneo		Philippines	
									Sarawak	Sabah	Palawan	Mindanao
Anathana (1)	*ellioti*											
Dendrogale (2)					*murina*				*melanura*	*melanura*		
Ptilocercus (1)						*lowi*	*lowi*		*lowi*	*lowi*		
Urogale (1)												*everetti*
Tupaia (10) (?)		*glis*	*glis*	*glis* *minor*	*glis*	*glis* *minor*	*glis* *minor* *javanica* *tana*	*glis* *javanica*	*glis* *minor* *dorsalis* *tana* *gracilis* *montana* *picta* *splendidula*	*glis* *minor* *dorsalis* *tana* *gracilis* *montana*	*glis*	

C. hippurus-group (but not *C. hippurus* Geoffroy, 1832 *perse*) occurring on Palawan and Mindanao. (*Nannosciurus melanotis* (Müller, 1838) is found in Borneo, Sumatra and Java, and other *Nannosciurus* are present in Mindanao and a few other islands of the Philippines. The related *Exilisciurus exilis* (Müller, 1838) is known from Borneo and Sumatra.) All of the squirrels listed for Sumatra occur in both Malaya and Sarawak, but the converse is not quite true, for *Dremomys* has apparently not been reported from Sumatra. Of the 8 entries for squirrels from Sumatra, Malaya and Borneo, 4 are presumably absent from Java (*C. prevosti*, *C. hippurus*, *Sundasciurus* Moore, 1958, and *Rhinosciurus* Gray, 1843). It should be noted that no squirrels (nor tupaiids) have ever been reported from Luzon, and that sciurids are unknown east of the vicinity of Celebes.

There are 8 groups or species of rats listed in Table 7 (facing p. 406), and only 1 of these, *Rattus* (*Stenomys*) *bowersi*, is wholly continental Asian, but as mentioned, a closely related species, *R.* (*S.*) *infraluteus*, is endemic to Sabah. The broadest range is exhibited by *R.* (*Maxomys*) *fulvescens* (Gray, 1847), which actually is found as far north and west as Nepal and Tibet, and south and east all the way to Sabah. *R.* (*Lenothrix*) *rajah* (Thomas, 1894) and *R.* (*L.*) *surifer* (Miller, 1900) have often been misidentified or confused by mammalogists, at least until recently, and hence the 2 are regarded as a 'group' herein, occurring from Thailand to Palawan. Of the 3 species of rats listed as occurring in Malaya, Sumatra and Sarawak, one, *R.* (*L.*) *whiteheadi* (Thomas, 1894) is absent from Java.

Two insectivores are treated herein, *Hylomys suillus* Müller, 1839, the lesser gymnure, an erinaceid, which is found in all the areas cited save the Philippines, and *Crocidura* Wagler, 1832, species of which exist in all these countries, and many others in Asia and in Africa, etc.

B. Data on Distribution or Hosts of Siphonaptera

1. Pygiopsyllids in General

Inasmuch as *Medwayella*, *Lentistivalius* Traub, 1972 and *Stivalius* (s. str.) Jordan & Rothschild, 1922, are all pygiopsyllids, it is advisable to first make some generalizations about the distribution of that family of fleas, including material from the wealth of yet undescribed taxa at hand. Of the total of 33 genera (or species-groups) of pygiopsyllids of non-volant hosts known to me, 21 (63%) are found in New Guinea or Australia or both (Traub, in prep.). An additional genus of the Australian Region (*Pygiopsylla* Rothschild, 1906) is also known from Borneo. A total of 121 of 176 species (69%) of pygiopsyllids of such hosts are found in Australia or New Guinea. Seven genera occur in Indonesia or Borneo, and 5 in the Philippines. There is only 1 in the Palaearctic Region represented by a Japanese species of *Lentistivalius*, a wide-ranging genus known by a single species in Borneo (on tree-shrews), Malaya (on birds), Indian subcontinent (on shrews[1]) and in the Ethiopian Region of Africa (on rodents) (Traub, 1972a). There is now at hand a new species of murid-*Lentistivalius* from the Philippines. There is also an endemic African genus of 14 species,

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[1] *L. ferinus* (Rothschild, 1908) ranges to Nepal, where it may possibly enter the fringe of the Palaearctic Region.

TABLE 4

Distribution of some† genera and species-group of pygiopsyllid fleas known from the Oriental Region and Wallacea

	Medwayella	*Stivalius* (s. str.)	*Gryphopsylla*	*jacobsoni*-group	*mjoebergi*-group	*pomerantzi*-group	New genus	*celebensis*-group	*Pygiopsylla*
Yunnan and South China		1			1*				
Indo-China	2* (1)				1*				
Thailand	3^{3*}				1*				
Malaya	6^{3*} (1)			1*	1*				
Sumatra	3*			1*					
Java	3^{2*}	1*		1*					
Celebes								1	
Borneo	11^{3*} (4)		1	(1)*	1				1
Philippines	(2)	1*		(1)*		2	1		
Indian Subcont.		3							
Total No. Spp. 21		5	1	2	2	2	1	1	1

* = One species occurs in more than one area.
New species are in ( ).
† = *Lentistivalius* is far-ranging and hence treated in the text.

Genus
Medwayella
(21 spp.)
(Totals)
Macrostylop
(28 spp.)
(Totals)
Syngenopsyll
(3 spp.)
(Totals)
Paraceras
(10 spp.)†
(Totals)

Names in p
* = One ne
† = Includ
was from 'tro

TABLE 5

Distribution of species of genera of fleas which have representatives infesting squirrels in the Malayan and Southeastern Oriental Subregions

Genus	Himalayan or North Burma	South China Mountains	Ceylon	Taiwan	North Asia or Europe	Indo-China	Thailand	Malaya	Sumatra	Java	Borneo		Philippines	
											Sarawak	Sabah	Mindanao	Palawan
Meduwayella							*robinsoni*	*robinsoni*	*robinsoni*	*robinsoni*	*robinsoni*			
(21 spp.)						*thurmani*	*thurmani*							
							phangi	*phangi*			*phangi*			
								calcarata			*calcarata*			
								dryadosa		*dryadosa*				
											veruta	*veruta*		
								limi	*arcuata*	*javana*	*batibacula*			
						1 n. sp.		1 n. sp.	*angustata*		*loncha*	4 n. spp.	1 n. sp.	1 n. sp.
											rhaeba			
(Totals)						(2)	(3)	(6)	(3)	(3)	(6)	(5)	(1)	(1)
Macrostylophora	*hastata*					*hastata*	*hastata*	*hastata*						
(28 spp.)								*levis*	*levis*					
							euteles							
		euteles												
		liae		*liae*										
	fimbriata	*exilia*	*phillipsi*			*pilata*			*idoneus*			*borneensis*		
	lupata	*trispinosa*				*probata*			*sodalis*					
	uncinalis													
	heinrichi	*cuiae*												
				1 n. sp.*		1 n. sp.				2 n. spp.		3 n. spp.*	5 n. spp.	1 n. sp.
(Totals)	(5)	(5)	(1)	(2)		(4)	(2)	(2)	(3)	(2)		(4)	(5)	(1)
Syngenopsyllus							*calceatus*	*calceatus*	*calceatus*	*calceatus*				
(3 spp.)						1 n. sp.		1 n. sp.						
(Totals)						(1)	(1)	(2)	(1)	(1)				
Paraceras	(*hamatum*)			(*sauteri*)	(*melis*)	1 n. sp.	(1 n. sp.)	(1 n. sp.)		(*javanicum*)		(*pendleburyi*)		
(10 spp.)†					(*crispis*)									
(Totals)	(1)			(1)	(2)	(1)	(1)	(1)		(1)		(1)		

Names in parentheses indicate species which infest carnivores or rats, not squirrels.

* = One new species of *Macrostylophora* occurs both on Borneo and Taiwan, on *Dremomys*.

† = Includes *P. melinum* whose host and type-locality are unknown but which Jordan (1939) believed was from 'tropical Asia'.

and a Neotropical one of 5 species, but there are no known Nearctic taxa. Thirty of the 32 (94%) remaining genera are limited to the Australian, Wallacean or Oriental Regions, and only 3 occur on the Asian mainland, where they are relatively poorly represented insofar as concerns species. There are 170 species known to me in these 30 genera, and 137 (80%) of these are restricted to the Australo-Asian Archipelagoes.

A break-down of the genera (and species-groups representing unnamed genera) occurring in the Oriental Region and Wallacea is shown in Table 4. (*Lentistivalius* is deleted therefrom but has been treated above.) As can be seen, 11 species (52%) of the known total of 21 *Medwayella* are found in Borneo, but 3 of these also occur elsewhere. *Medwayella* is relatively rich in species in Malaya, where 6 (29%) have been reported, but the maximum number elsewhere is 3 (Thailand and Java). The low numbers in the other Oriental areas are noteworthy, even though the totals for Sumatra and Java probably reflect inadequate collecting. Enough field-work has been done in Thailand, Indo-China and Mindanao to indicate that the total number of *Medwayella* therein must be substantially lower than in Malaya or Borneo. Further, Malaya has been well studied, but it seems likely that additional new species of *Medwayella* await discovery in Borneo, especially in Kalimantan and Sarawak. Additional data on the distribution of *Medwayella* are presented in Tables 5 and 7 where the hosts are treated.

All of the other genera are represented by but 1 or 2 species, with the exception of *Stivalius s. str.*, which consists of 5 species (all on the subgenus *Rattus*), of which 3 are Indian. It is noteworthy that the *S. jacobsoni* group and the *S. mjoebergi* group, both listed for 2 species, each includes a widespread species which occurs on the mainland, namely, *S. jacobsoni* (Jordan & Rothschild, 1922) and *S. klossi* (Jordan & Rothschild, 1922) respectively. The new species in Borneo is likewise found on Palawan. It is stressed that virtually no fleas are known from Celebes, and I am certain that a rich fauna of pygiopsyllids awaits discovery there.

2. Callosciurine Fleas

Because *Medwayella* is so intimately associated with Oriental squirrels, data on squirrel-fleas of that Region are presented in Tables 5 and 6. However, it should be borne in mind that squirrels are common in the Palaearctic and Nearctic Regions, and even in the Ethiopian Region as well, and that there they carry different kinds of fleas. Such data on northern and African squirrels are summarized later (p. 410 and Tables 8 and 9).

In Table 5 are listed the species of callosciurine fleas which occur in the Burmo-Chinese and Malayan Subregions, as well as other members of those genera which infest other hosts in the areas specified. In the latter category are fleas of rats and carnivores, and the names of these fleas are shown in parentheses. Of the remainder, which are sciurid-fleas, *Macrostylophora fimbriata* (Jordan & Rothschild, 1921) is a Himalayan flying-squirrel flea. (Other squirrel-fleas, besides those listed, occur in the Palaearctic areas cited, e.g. *Monopsyllus* Kolenati, 1857, but since such genera are not represented in these Oriental Subregions, they are deleted from the Table. Fleas of funambuline squirrels are likewise unlisted, since either they are absent from the pertinent Subregions, e.g. *Funambulus* Lesson, 1835, or else are not yet known to have specific fleas, if any at all, i.e. *Ratufa* Gray, 1867.[2]) In the approximate geographic area being treated, there are two genera of squirrels for which we regrettably have no data, namely the monotypic *Rheithrosciurus*[2] in Borneo and *Prosciurillus* Ellerman, 1947[2] (3 species) in Celebes.

There are 21 species of *Medwayella* in Table 5, and 5 of these are found in more than one area. *M. robinsoni* (Rothschild, 1905) ranges from Thailand to Sarawak. *M. thurmani* Traub, 1972, is reported from Indo-China and Thailand. *M. phangi* Traub, 1972, occurs in Malaya and Sarawak. *M. calcarata* Traub, 1972, occurs in Malaya and Sarawak, while *M. dryadosa* Traub, 1972, heretofore known only from Malaya, has just been discovered in Java, subsequent to the description of the species in the first article in this series. Three of the Malayan species are found in Sarawak.

The ceratophyllid genus *Macrostylophora* Ewing, 1929, is a characteristic parasite of callosciurine squirrels throughout the Burmo-Chinese and Malayan Subregions, and in at least parts of the Indian Subregion, ranging to Ceylon. It extends into extremities of the Palaearctic Region into what is here termed the Eastern Palaearctic Subregion rather than Oriental Region (despite the position on the map), namely the mesic mountains of the Indian subcontinent and Formosa. A total of 10 species of *Macrostylophora* have been described from the Himalayan-North Burma-southern China area (which includes both Palaearctic and Indian elements) despite the fact that relatively little collecting of squirrel-fleas has been undertaken there. One of these northern species, namely *M. hastata* (Jordan & Rothschild, 1921) ranges as far east and south as Indo-China and Malaya. Although we have intensively collected squirrel-fleas in Malaya, only 2 species have been found there, and but 4 in Sabah. The finding of 5 species on Mindanao (all new) is worthy of note. A good example of a species of flea sharing the range of its host is provided by *M. liae* Wang, 1957, which is found on *Tamiops swinhoei* (Milne-Edwards, 1874) in both southern China and Formosa. *Macrostylophora* undoubtedly infests squirrels in Sarawak despite the dearth of reports, and it would not be surprising if it accompanied *Callosciurus prevosti* and *C. notatus* to Celebes.

The genus *Syngenopsyllus* Traub, 1950, includes *S. calceatus* (Rothschild, 1905) which ranges from Thailand to Sumatra and Java, and 2 new species, 1 from Malaya and 1 from Indo-China. There is a total of 10 species in the genus *Paraceras* Wagner, 1916, but only 1, an undescribed species from Indo-China, infests squirrels. The remainder parasitize carnivores such as badgers or civets, and rats, and 3 of these are Palaearctic.

Table 6 deals with the fleas of the callosciurine hosts for which we have reasonably good data on Siphonaptera, listing the species by name or by rather self-evident abbreviations. New species are given alphabetical designations to permit discussion.

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[2] Moore (1959) placed the genus *Ratufa* off by itself in a special tribe, the Ratufini. Simpson (1945) and Morris (1965) included it in Funambulini. Another change made by Moore was to remove *Prosciurillus* from the Sciurini and place it in the Callosciurini. Both Moore and Simpson, using different characters, concluded that *Rheithrosciurus* (which Moore in 1959 and 1961*a* spelled *Reithrosciurus*) belongs in the Sciurini, and this means that this rarely-collected Borneo squirrel is more than 3000 miles distant from its nearest relative. This remarkably disjunct distribution is of great interest in zoogeography.

	Squi
1.	*Callo*
2.	*Callo*
3.	*Callo*
4.	*Callo*
5.	*Callo*
6.	*Callo*
7.	*Sund* *S. lo*
8.	*Tam*
9.	*Drer*
10.	*Lari*
11.	*Men*
12.	*Rhin*

+ = M

TABLE 6

Major fleas of tree-squirrels (Nos 1–5), scansorial squirrels (Nos 7–8) and ground-squirrels in certain areas of the Oriental Region

						Borneo		Philippines	
Squirrels	Indo-China	Thailand	Malaya	Java	Sumatra	Sarawak	Sabah	Palawan	Mindanao
1. *Callosciurus caniceps*	+	+	*Med. rob.* *Syn. cal.* +						
2. *Callosciurus hippurus*			*Med. rob.* +		+	+	*Med.* n. sp. A +		
3. *Callosciurus notatus*		+	*Med. rob.* *Syn. cal.* +	*Med. rob.* *Syn. cal.* +	*Med. rob.* +	*Med. rob.* +	*Macro.* n. sp. A +		
4. *Callosciurus nigrovittatus*		*Med. rob.* +	*Med. rob.* +	*Med. rob.* *Med. jav.* +	*Med. ang.* +	+	*Macro.* n. sp. B +		
5. *Callosciurus prevosti*			*Med. rob.* +		+	+	*Med.* n. sp. A +		
6. *Callosciurus* (Others)	+	*Macro. hast.* +	+	+	+	*Med. phangi* +	+	*Med.* n. sp. B *Macro.* n. sp. C +	*Med.* n. sp. C 4 *Macro.* n. spp. D–G +
7. *Sundasciurus tenuis* or *S. lowi*		+	*Med. rob.* *Med. phangi* *Macro. levis* +		+	*Med. loncha* +	*Med. veruta* *Med.* n. sp. D +		
8. *Tamiops macclellandi*	*Macro. hast.* *Macro. pil.* *Macro. prob.* +	*Macro. hast.* +	*Macro. hast.* +						
9. *Dremomys* (species)	*Med.* n. sp. E *Macro.* n. sp. H +	+	*Med.* n. sp. F *Macro. hast.* +			+	*Lent. vom.* *Macro. born.* *Macro.* n. sp. I +		
10. *Lariscus insignis*			*Med. rob.* *Med. calc.* *Med. dry.* +	*Med. rob.* *Med. dry.* *Macro.* n. sp. J *Macro.* n. sp. K +	*Med. ang.* (?) +	*Med. calc.* *Med. bati.* +			
11. *Menetes berdmorei*	*Med. thurm.* *Med.* n. sp. E +	*Med. thurm.* *Macro. hast.* +							
12. *Rhinosciurus laticaudatus*			*Med. rob.* *Med. dry.* *Med. limi* +		+	*Med. calc.* +	+		

+ = Mammal present in area indicated.

The distribution of the hosts is indicated by a '+', and it is stressed that in many instances data on Siphonaptera are lacking for certain important regions, in cases where the squirrels are major hosts elsewhere. This is true, for example, for *Rhinosciurus* in Sumatra and Borneo, *Dremomys* in Sarawak, most hosts in Indonesia, and tree-squirrels in Sarawak.

As shown in Table 6, the various species of *Callosciurus* (all tree-squirrels) are major hosts of *M. robinsoni* in Malaya, and this probably will prove to be the case throughout the range of that flea. A new species of *Medwayella* appears to be prevalent on *Callosciurus* on Palawan and a second species fairly common on such squirrels on Mindanao. *S. calceatus* has also been collected from a variety of*Callosciurus* from Thailand to Java, but actually these represent only a few records,and it may even be that this species will prove to be a flying-squirrel flea, or a nest-flea of squirrels living in very tall trees (Traub, 1972b). *Macrostylophora hastata*, which at a minimum ranges from Nepal to Indo-China, is not very host-specific, infesting several species of *Callosciurus* and *Dremomys*, etc. In marked contrast, 2 new species from Sabah (Mt Kinabalu) are highly specific: over 95 % of the long series of '*Macro. A*' were collected from *C. notatus* and 90 % of '*Macro. B*' were from *C. nigrovittatus* Horsfield, 1824, even though the 2 species of infested squirrels not only came from the same areas, but often the same trees. Moreover, the exceptions (5 % for species '*A*' and 10 % for species '*B*') came from other genera of squirrels, such as *Dremomys* or *Glyphotes*.

The specificity of these *Macrostylophora* for *C. notatus* and *C. nigrovittatus* in Sabah seems especially significant in view of the fact that these squirrels are not known to be infested with any *Macrostylophora* in Malaya, and, indeed, are intimately associated there with a species of flea which is apparently absent from Sabah, namely *Medwayella robinsoni*. No other species of flea was represented in the extensive collections from Malayan *C. nigrovittatus*, and 99 % of the fleas from *C. notatus* there were *M. robinsoni* (Traub, 1972a). The other species of *Medwayella* occurring in Malaya are primarily fleas of ground-squirrels, as mentioned in the first article in this series.

The ground-squirrel *Dremomys* occurs on the Asian mainland from Nepal to south China to Indo-China and Malaya (with a total of 3 or 4 species) and is found in Borneo (1 endemic species) and Formosa (1 endemic species) but it has not been reported in Indonesia. Under these circumstances, it is not surprising that the Bornean, Malayan and Indo-Chinese species of fleas known to infest these various *Dremomys* are all different. The fact that a new species of *Macrostylophora* from *Dremomys* on Mt Kinabalu apparently occurs as a subspecies in Formosa on another species of *Dremomys* is of interest.

The 3 species of *Medwayella* associated with *Rhinosciurus* in Malaya have not been found on this host elsewhere, but, unfortunately, there are few records of any fleas from this host in other countries, so these data cannot be properly evaluated. A greater number of species of *Medwayella* (7) appear to infest the ground-squirrel *Lariscus insignis* than any other host. Moreover, 3 of these have been found in other countries besides Malaya, as indicated.

In contrast to the apparent predilection of *Medwayella* for ground-squirrels, *Macrostylophora* is intimately associated with truly arboreal squirrels. Thus, only 1 species, *M. levis* (Jordan & Rothschild, 1922) is common on a scansorial species. (As noted, only 1 infests flying-squirrels.)

It should be noted that although none of the fleas listed for Sarawak in Table 6 were recorded for Sabah, and vice versa, there are 2 species which occur in both areas, as mentioned below.

3. Fleas of Tupaiids, Rats and Insectivores

Table 7 deals with the fleas of certain tupaiids, rats and insectivores in the Burmo-Chinese and Malayan Subregions. The various species of *Tupaia* seem to be important hosts of *Medwayella* wherever they have been examined, but almost invariably those fleas seem to be more prevalent on callosciurines in the area than on *Tupaia*. Thus, in Malaya, no *M. calcarata* and only 2% of the *M. limi* Traub, 1972, and 10% of the *M. dryadosa* came from *Tupaia* (Traub, 1972a). The only instances to the contrary concern species known from only a few specimens, or in areas where data are lacking on *Callosciurus* (e.g. Sarawak). Similarly, throughout its range, *Stivalius klossi* is more abundant on *Rattus* than on *Tupaia*. However, on Mt Kinabalu, *Lentistivalius vomerus* Traub, 1972, and *S. mjoebergi* Jordan, 1926, were more plentiful on *Tupaia* than on other hosts. The former species was also taken on the tree-shrew *Dendrogale* fairly frequently.

The geographic records on *Tupaia* do not modify the picture shown by the callosciurines, except in two instances. *S. mjoebergi* was originally described from *Tupaia* on Mt Murud in northern Sarawak, but was later found by our teams and colleagues to be abundant on Mt Kinabalu and Mt Trus Madi in Sabah. It has not been reported farther south in Sarawak, but nevertheless must be listed as occurring in both areas. The only other indigenous species known to do so is *Medwayella veruta* Traub, 1972. First found near the base of Mt Kinabalu, the species was later collected by us in Kapit District, Sarawak (Traub, 1972a). This latter record (which apparently represents a distinct subspecies) is based upon 1 specimen from *Tupaia*, personally collected at about 100 ft elevation on an intensive collecting trip of several weeks' duration, during which time several hundred squirrels, rats and tree-shrews were carefully examined for fleas. This illustrates how scarce fleas can be in the humid tropical lowlands, at least at times, and emphasizes that the gaps in our knowledge of the zoogeography of fleas are not merely due to failure to examine mammals in certain areas.

The current Bornean records of fleas from rats and insectivores, like those from the squirrels and most of those from *Tupaia*, also suggest there may be some basic differences in the faunae of Sarawak and Sabah, since all of the species listed are for Sabah alone. Collections from the montane regions of Sarawak may modify this impression somewhat, for the endemic species of *Sigmactenus* Traub, 1950, occurring in New Guinea and the Philippines are widespread and abundant on the subgenus *Rattus* in the mountains, and it would be expected that this was true for the Borneo species as well.

The data in Table 4 are also relevant regarding the distribution of rat-pygiopsyllids since 6 of the 9 taxa are essentially rat-fleas and, in addition, 1 species of the *Stivalius mjoebergi*-group, namely *S. klossi*, infests these murines. The rat forms

H
1. *Tupaia* (s
2. *Dendrogal* (Tree-shre
3. *Rattus* (*Le* *alticola*-gr
4. *Rattus* (*Le* *R. surifer*
5. *Rattus* (*Le*
6. *Rattus* (*M*
7. *Rattus* (*R*
8. *Rattus* (*Ra*
9. *Rattus* (*St*
10. *Rattus* (*St*
11. *Rattus* (sp
12. *Hylomys s*
13. *Crocidura*

+ = Mamma

TABLE 7

Major fleas of tree-shrews (tupaiids) (Nos 1–2), rats (Nos 3–10) and insectivores in certain areas of the Oriental Region

Hosts	Indo-China	Thailand	Malaya	Java	Sumatra	Borneo		Philippines	
						Sarawak	Sabah	Palawan	Mindanao
1 *Tupaia* (species) (Tree-shrews)	*Med. thurm.* *Med.* n. sp. E *Stiv. klossi* +	*Med. thurm.* *Stiv. klossi* +	*Med. rob.* *Med. phangi* *Med. dry.* *Stiv. klossi* +	*Med. jav.* (?) +	*Med. arc.* (?) +	*Med. phangi* *Med. ver.* *Stiv. mjoe.* +	*Med. ver.* *Med.* n. sp. D *Lent. vom.* *Stiv. mjoe.* *Macro. born.* +	*Med.* n. sp. B +	
2. *Dendrogale melanura* (Tree-shrew)						+	*Lent. vom.* +		
3. *Rattus* (*Lenothrix*) *alticola*-group							*Sig. alt.* *Gryph. hop.* +		
4. *Rattus* (*Lenothrix*) *rajah* or *R. surifer*		*Stiv. klossi* +	*Stiv. klossi* *Roths. smiti* +	+	+	+	*Sig. alt.* +	+	
5. *Rattus* (*Lenothrix*) *whiteheadi*		+	+		+	+	*Gryph. hop.* +		
6. *Rattus* (*Maxomys*) *fulvescens*	+	+	*Stiv. jacob.* +	*Stiv. jacob.* *Roths. kop.* +	+	+	*Stiv.* n. sp. A +		
7. *Rattus* (*Rattus*) *baluensis*							*Pyg. tip.* +		
8. *Rattus* (*Rattus*) (species)	*Stiv.* (*S*) *apor.* *X. vex.* +	*Stiv.* (*S*) *apor.* *X. vex.* *Parac.* n. sp. A +	+	*Stiv.* (*S*) *cog.* *Stiv. jacob.* *Neo. sond.* +	+	+	+	+	*Stiv.* (*S*) *cog.* *Stiv. pom.* *X. vex.* *Sig. wer.* +
9. *Rattus* (*Stenomys*) *bowersi*	*Neo. dispar* *Neo. avida* *Neo. tric.* +	*Neo. dispar* +	*Neo. dispar* *Parac.* n. sp. B +						
10. *Rattus* (*Stenomys*) *infraluteus*							*Neo. luma* +		
11. *Rattus* (species)	*Stiv. klossi* +	*Stiv. klossi* +	*Stiv. klossi* *Stiv. jacob.* *Parac* n. sp. B +	*Stiv. klossi* *Stiv. jacob.* *Neo.* n. sp. *Roths. kop.* +	*Stiv. klossi* *Stiv. jacob.* +	+	*Stiv.* n. sp. A *Sig. alt.* +	*Stiv.* n. sp. A +	*Sig. wer.* +
12. *Hylomys suillus* (Gymnure)	+	+	+	*Crat. bart.* +	+	+	*Crat. audyi* *Crat. crypt.* +		
13 *Crocidura* (Shrews)	+	+	*Pal. apsid.* +	*Pal. laxata* +	+	+	+	+	+

+ = Mammal present in area indicated.

are *Stivalius* (*s. str.*); *Gryphopsylla* Traub, 1957;[3] the *S. jacobsoni*-group; the *S. pomerantzi*-group; the new genus from the Philippines and *Pygiopsylla* (on Borneo, at least).

Many of the species listed for rats in Table 7 (and alluded to in Table 4) have a fairly broad range and are relatively non-specific, e.g. *S. klossi*, which is found on various subgenera and species of forest-rats from Indo-China to Sumatra, and *S. jacobsoni*, which is known from Malaya, Sumatra and Borneo and infests similar hosts. The dearth of records of *S. klossi* from members of the subgenus *Rattus* is notable, even though occasional specimens are found on the wild forms. The new species on a variety of rats on Mt Kinabalu exists as a subspecies on Palawan and apparently is a derivative of *S. jacobsoni*. The rat with the maximum range is *R.* (*Maxomys*) *fulvescens* (Indo-China to Sabah), but no records of its fleas exist for much of the territory. The new genus listed in Table 4 is from Mindanao and presumably is a parasite of an endemic genus of rat and is related to the pygiopsyllids associated with New Guinea and the *S. celebensis*-group of New Guinea.

Rats of the subgenus *Rattus* are found throughout the Oriental, Wallacean and Australian Regions, and many indigenous species are represented, as well as commensal ones. As expected, their fleas include endemic, restricted and wide-spread species. *Stivalius* (*S.*) *aporus* Jordan & Rothschild, 1922, apparently as subspecies of an Indian form, exists in southern China, Indo-China and Thailand (Traub, 1972a). *S.* (*S.*) *cognatus* Jordan & Rothschild, 1922, is known from Java and the Philippines (Mindanao and Luzon), again as subspecies, and probably occurs elsewhere in the Subregion. *Stivalius pomerantzi* Traub, 1951, apparently represents a distinct genus and has been found on several of the islands of the Philippines (Mindanao, Negros and Leyte). *Pygiopsylla tiptoni* Traub, 1957, a characteristic flea of *R. baluensis* (Thomas, 1894), is indigenous to Mt Kinabalu, and its nearest known relatives are in New Guinea and Australia. (It appears significant that Misoune (1969) presumably regarded this rat as belonging in the subgenus *Bullimus* Mearns, 1905, near *R. xanthurus* (Gray, 1867) of Celebes, and not in the subgenus *Rattus*. Sody (1941) and others treated it as a subspecies of *R. rattus* (Linnaeus, 1758). Ellerman (1941) and Medway (1963) viewed it as a full species in the subgenus *Rattus*, and Medway (p. 122) emphasized it 'is very distinct . . . separated . . . by both morphology and habit'.)

Several non-pygiopsyllids are associated with the subgenus *Rattus*. The one with the broadest range is *Xenopsylla vexabilis* Jordan, 1925 (Pulicidae) which has been collected in Australia, New Guinea, Mindanao, Java, Indo-China and Thailand. The main host on the mainland is *Rattus berdmorei* (Blythe, 1851) (which is in the subgenus *Bullimus* according to Misoune (1969) but in the subgenus *Berylmys* Ellerman, 1947, fide Ellerman & Morrison-Scott (1951)). However, it is also found on the subgenus *Rattus* on Continental Asia, and primarily so, usually on commensal forms, on the Pacific Islands. *X. vexabilis* has also been introduced into Hawaii via commensal rats. It should be noted that there are other *Xenopsylla* Glinkiewicz, 1907, in the Burmo-Chinese Subregion and the Australian Region which are endemic (and specialized) and which are not associated with the subgenus *Rattus*, namely *X. papuensis* (Jordan, 1933) on certain species of the phloeomyine murid genus *Pogonomys* Milne-Edwards, 1877, in New Guinea and a new species on an indigenous rat in the mountains of Luzon.

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[3] NEW STATUS. This was heretofore treated as a subgenus of *Stivalius*.

4. *Leptopsylla* and Allies

Of special interest is the occurrence of members of the family Leptopsyllidae in the Burmo-Chinese and Malayan Subregions, 2 of which, *Sigmactenus werneri* Traub, 1950, and *S. alticola* Traub, 1954, are listed in Table 7. The genus *Sigmactenus* is akin to *Leptopsylla* Jordan & Rothschild, 1911, along with *Peromyscopsylla* I. Fox, 1939, and the 3 genera include a total of 36 species. Of this total, 26 are Palaearctic, 3 Oriental, 1 Australian, 1 Ethiopian, 6 Nearctic, and 2 are Holarctic (Traub, in prep.). There are 3 species of *Sigmactenus* and all infest rats: *S. werneri*, on Mindanao and Negros in the Philippines; *S. alticola*, on Mt Kinabalu, etc., in Sabah, and *S. toxopeusi* Smit, 1953, in New Guinea. The existing records of *S. alticola* are from forest-rats, primarily *R.* (*Lenothrix*) *alticola* in a habitat where there were no rats of the subgenus *Rattus*. At least one of the others (*S. werneri*) is common on (*Rattus*), and this may prove to be the case for *S. alticola* in other parts of Borneo.

Sigmactenus is most closely allied to *Leptopsylla* (*Pectinoctenus*) Wagner, 1928, a Palaearctic taxon, which includes 6 species, 5 of which infest the murine *Apodemus* Kaup, 1829, and 1 of which parasitizes cricetids. The subgenus *Leptopsylla* includes 9 species of which 8 are Palaearctic (5 on murines) and 1 Ethiopian (on rats). Only 1 of the 18 species of *Peromyscopsylla* infest murines; 12 occur on microtines and 7 of these are Nearctic and 2 Holarctic; the remaining 8, Palaearctic. There are 4 Nearctic *Peromyscopsylla* ex *Peromyscus* Gloger, 1841, and 1 Palaearctic species associated with *Calomyscus* Thomas, 1905, a cricetine.

Except for the 2 species of *Sigmactenus*, the only leptopsyllid allied to *Leptopsylla* which is known from the Oriental Region is a species of *Peromyscopsylla* which is either *P. himalaica* (Rothschild, 1915) or a sibling derivative thereof, resident on *Rattus* in the mountains of central Luzon. *P. himalaica* is a far-ranging species known from Taiwan, Japan, and northern India, where it infests *Rattus* or *Apodemus*. (This is apparently the first faunal record in the Philippines of a non-commensal species with Palaearctic affinities, and it is noteworthy that along with this *Peromyscopsylla*, there was taken another leptopsyllid, *Frontopsylla nakagawai* Kumada & Sakaguti, 1959, an amphipsylline, previously known from Japan and Taiwan, where it infests *Apodemus*.)

5. *Neopsylla* and Allies

Another taxon in Table 7 which is of definite northern (Palaearctic) affinity is the hystrichopsyllid genus *Neopsylla* Wagner, 1903 (Neopsyllinae). The 11 genera of this subfamily are all allied and encompass a total of 88 species for which I have data. Nine of the genera, including 57 of the species, are found in either the Nearctic or Palaearctic Regions (or both) and nowhere else. Only 2 genera, *Neopsylla* and *Rothschildiana* Smit, 1952, occur in the Oriental Region, and these merit further consideration. There are 29 species of *Neopsylla*, for which we have reliable host-data, and of these, 1 is Nearctic, 20 are Palaearctic and 9 are Oriental (of which 1 also occurs in the Palaearctic Region). Eight of the 9 Oriental species are parasites of rats; the exception is the south Chinese species which also is Palaearctic. Fifteen of the 29 *Neopsylla* under discussion are rat-fleas; the remainder infest sciurids and cricetines. The genus *Neopsylla* was divided into two groups, the *N. stevensi*-group and the *N. setosa*-group, purely on the grounds of leg-chaetotaxy by Hopkins & Rothschild (1962), but, interestingly enough, the classification extends to the hosts as well, for the *N. stevensi*-group includes all the *Rattus*-fleas. Seven of these rat-*Neopsylla* are Palaearctic and 8 are Oriental. Five rat-*Neopsylla* are listed in Table 7: 3 from Indo-China, of which *N. dispar* Jordan, 1932, extends into Malaya; *N. sondaica* Jordan, 1931, on Java and *N. luma* Traub, 1954, in Sabah. (The remaining 3 are from southern China.) The 3 Indo-Chinese species infest *R.* (*Stenomys*) *bowersi*, as does *N. dispar*. *N. luma* is closely related to *N. dispar*, and it is of interest that its host, *R.* (*S.*) *infraluteus*, is allied to *R.* (*S.*) *bowersi*. The true hosts of *N. sondaica* are unknown.

The second Oriental neopsylline genus, *Rothschildiana*, is essentially a somewhat specialized *Neopsylla* and is known from 2 species: 1 Malayan, associated with the *R.* (*Lenothrix*) *rajah*-group, and the other, with *R.* (*Maxomys*) *fulvescens* on Java. All together, a total of 11 species of Neopsyllines occur in the Oriental Region, 4 of these in the Malayan Subregion.

6. Ceratophyllid Rat-Fleas

In general, there are relatively few ceratophyllid fleas infesting rats. One exception is the genus *Nosopsyllus* Jordan, 1933, which, while present in India, is not known to extend into the Malayan or Burmo-Chinese Regions. (It may be present in Burma, etc.) *Paraceras* is another, and as noted, 7 or 8 of the 10 species are Oriental, but at least 1 of the Palaearctic species is European. There are 2 *Paraceras* listed in Table 7, both new to Science. One is from an unidentified species of the subgenus *Rattus* in Thailand, and the second a common parasite of *R.* (*M.*) *fulvescens* in the mountains of Malaya.

7. Insectivore-Fleas

Relatively little is known about insectivore-fleas in the Oriental Region in general and especially in the Southeastern and Malayan Subregions. Two genera have been reported for the Malayan Subregion, however, viz., the leptopsylline *Cratynius* Jordan, 1933, and the hystrichopsyllid *Palaeopsylla* Wagner, 1903. *Cratynius* is presumably a fairly specific flea of the lesser gymnure *Hylomys suillus*, a monotypic erinaceid that ranges from Indo-China to Borneo, but the only records of the fleas are from Java (1 species) and Sabah (2 species). Except for *Palaeopsylla*, there are no Ctenophthalminae in the Oriental Region, and 23 of the 27 contemporary *Palaeopsylla* occur in the Palaearctic Region. There are but 5 known from the Oriental Region, and 1 of these is Palaearctic as well. Three of the Oriental ones are from south China. The Malayan and Javanese species (Table 7) were both collected on shrews in the mountains.

8. Squirrel-Fleas in General

As a basis for discussing the possible origins and affinities of *Medwayella*, it is advisable to consider the distribution and background of all genera of fleas which include species infesting tree-squirrels (including flying-squirrels). Such data are summarized in Tables 8 and 9, but it should be noted that the fleas of spermophiles, chipmunks and marmots are deleted therefrom because such hosts, by virtue of their nesting underground, and their intimate contact with the habitat of other ground-level rodents, have acquired fleas that are characteristic of, or akin to, those of such neighbouring mammals. *Xerus* Ehrenberg, 1833, and other African ground-squirrels are not represented because their flea fauna is insufficiently known and they too have acquired some atypical fleas.

As can be seen from Table 8, there is a rich fauna of fleas associated with tree-squirrels and semi-arboreal squirrels, e.g. 22 genera, representing 3 families and encompassing 109 species (out of the total of 293 belonging to those genera). It should be borne in mind, however, that the distribution indicated pertains to the genus as a whole, and not merely to the component infesting squirrels. Thus, in the case of the pygiopsyllid *Lentistivalius*, the single species on squirrels is found in Borneo, but the genus includes African and Japanese species on other hosts. Similarly, the genus *Monopsyllus* is Holarctic in the sense that representatives are found in the Nearctic and Palaearctic Regions, but only 1 of the species is truly Holarctic (namely *M. tolli* (Wagner, 1901) on *Ochotona* Link, 1795). The only Holarctic squirrel-flea is *Tarsopsylla octodecimdentata* (Kolenati, 1863).

Only 3 of the 16 recognized families of Siphonaptera have fleas characteristically infesting arboreal or semi-arboreal squirrels, namely the Hystrichopsyllidae, Pygiopsyllidae and Ceratophyllidae. There are 45 genera of Hystrichopsyllidae, and 33 (74%) of these are found in the 'holarctic' regions, with 12 (27%) in the border or transitional parts of those Regions, but with only 4 (9%) occurring in the Oriental Region (Traub, in prep.). (Some of these genera are found in more than one area, e.g. 2 of the Oriental hystrichopsyllid genera are also found in the Palaearctic, and 1 of those is Holarctic.) The Ceratophyllidae is essentially a northern family, i.e. 28 of 31 (90%) genera infesting non-volant hosts are found in the northern Regions, while only 5 (16%) are Oriental, and 3 of those are Palaearctic as well. (Additional generalizations about the northern affinities of ceratophyllids are presented in the Discussion (p. 423). As has been shown, the pygiopsyllids are very poorly represented in the north, with only 1 species of 1 genus being Palaearctic and none Nearctic.

The association with squirrels is relatively rare in the Hystrichopsyllidae (in only 4 of 45 genera—none Oriental) and Pygiopsyllidae (2 of 33 genera). In contrast, squirrel-fleas are known in 16 genera of Ceratophyllidae, and of the total of 196 species of fleas in such genera, 81 actually infest squirrels. It also seems significant that the hystrichopsyllid genera associated with squirrels are presumably nest-fleas, and that in each case only 1-2 of the species are involved (e.g. 2 of 52 *Rhadinopsylla* Jordan & Rothschild, 1912), the remainder being associated with other hosts. Similarly, among pygiopsyllids, 4 of the 5 known *Lentistivalius* para-

TABLE 8

Genera of Siphonaptera with species infesting arboreal or scansorial squirrels

Squirrel-fleas Genera and their distribution		Numbers of fleas and their major hosts		
		Total in genus or genera	On squirrels*	On other hosts
Hystrichopsyllidae	4 genera	71	6	65
Conorhinopsylla	(Nests) Nearctic	2	1	1 (*Neotoma*)
Epitedia	(Nests) Nearctic	8	1	7 (*Neotoma, Peromyscus*)
Megarthroglossus	(Nests) Nearctic	9	2	7 (*Neotoma*)
Rhadinopsylla	(Nests?) Holarctic	52	2	50 (Microtines, Cricetines)
Pygiopsyllidae	2 genera	26	22	4
Lentistivalius	Ethiopian, Oriental and Palaearctic	5	1	4 (Birds, Shrews, Murines, *Tupaia*)
Medwayella	Oriental	21	21	1 (?) (*Tupaia?*)
Ceratophyllidae	16 genera	196	±81	±112
Aenigmopsylla	Palaearctic	1	1	0
Brevictenidia	Palaearctic	1	1	0
Hollandipsylla	(Borneo)	1	1	0
Kohlsia	Temp. Mid. Amer. and Transitional	21	1	20 (Peromyscini)
Libyastus	Ethiopian	15	14	1 (Dormouse)
Macrostylophora	Oriental and Palaearctic	28	28	0
Monopsyllus	Holarctic	22	6	14 (Chipmunks, Cricetines)
Nosopsyllus	Palaearctic, Oriental and introduced	46	6	40 (Gerbillines, Murines, etc.)
Opisodasys	Nearctic	9	7	2 (*Peromyscus*)
Orchopeas	Nearctic, including Temp. Mid. Amer.	13	7	6 (*Peromyscus, Neotoma*)
Paraceras	Palaearctic and Oriental	9	1	8 (Carnivores, Rats)
Pleochaetis	Temp. mid. Amer. and Transitional	23	1 (2?)	22 (21?) (Peromyscini)
Syngenopsyllus	Oriental	3	3	0
Tarsopsylla	Holarctic	1	1	0
New genus No. 1	Palaearctic	1	1	0
New genus No. 2	Palaearctic	1	1	0

* = Excludes chipmunks, spermophiles, marmots, *Xerus* ground-squirrels, etc. (flying-squirrels *are* included).

sitize non-sciurids, but all of the 21 species of *Medwayella* infest squirrels. In the ceratophyllids, there is unanimity in the large genus *Macrostylophora* in this regard, while 14 of 15 *Libyastus* Jordan, 1936, and 7 of 9 *Opisodasys* Jordan, 1933, have squirrels for hosts. As Jellison has pointed out (1945), 4 genera of North American Siphonaptera, namely *Conorhinopsylla* Stewart, 1927, *Monopsyllus*, *Opisodasys* and *Orchopeas* Jordan, 1933, have 1 or more species occurring on tree-squirrels, and 1 or more on *Peromyscus* or *Neotoma* Say & Ord, 1825 (Cricetinae, Peromyscini). We now realize the *Epitedia* Jordan, 1938, *Megarthroglossus* Jordan & Rothschild, 1915, *Pleochaetis* Jordan, 1933, and *Kohlsia* Traub, 1950, are also in this category, as is *Rhadinopsylla*. The phenomenon of joint infestation of sciurid and peromyscine hosts by a single genus thus occurs in both Ceratophyllidae and Hystrichopsyllidae.

In some instances only a minority of the ceratophyllid species are involved in the relationship with squirrels, viz., 1 or 2 of 23 *Pleochaetis*, 1 of 21 *Kohlsia*. It is of interest that the squirrel-infesting *Nosopsyllus* are all in the Indian Subregion (where they infest *Funambulus*, a lowland group of 'palm-squirrels'), whereas the bulk of the 46 species are on murines or, in xeric areas, on gerbillines.

It should be noted that some of the ceratophyllid genera are known only from fleas associated with flying-squirrels, namely *Hollandipsylla* Traub, 1953, on *Hylopetes* Thomas, 1908, and the 2 new genera listed as No. 1 and No. 2, which are from Pakistan, on *Hylopetes* and *Petaurista* Link, 1795, respectively, in an area where ordinary tree-squirrels are unknown. In certain instances, a few of the species of a genus infest flying-squirrels while the bulk of them parasitize tree-squirrels, e.g. 2 of the 7 squirrel-*Opisodasys* (*O. pseudarctomys* (Baker, 1904) and *O. vesperalis* (Jordan, 1929)); 1 of the 28 *Macrostylophora* (*M. fimbriata*); 1 of the 7 *Orchopeas* of squirrels, namely, *O. bolivari* Barrera, 1955 (new status)[4]; and 1 of the pertinent 6 *Monopsyllus* (*M. argus* (Rothschild, 1908)). The Holarctic monotypic *Tarsopsylla* Wagner, 1927, may turn out to be a flea of flying-squirrels. (While the majority of records of the hystrichopsyllid *Rhadinopsylla japonica* Sakaguti & Jameson, 1956, are from flying-squirrels, I believe that this species is really a flea of the nests of such hosts.)

True nest-fleas appear to be rare among the species of Ceratophyllidae infesting sciurids. *Hollandipsylla* may be one. The status of *Syngenopsyllus*, *Libyastus*, *Tarsopsylla* and the 2 *Opisodasys* parasitizing flying-squirrels have been discussed in the second article in this series and their special modifications may be adaptive and correlated with the habits of the hosts.

The zoogeographic distribution of the genera which possess species infesting arboreal and semi-arboreal squirrels is summarized in Table 9. Here the picture is complicated by the fact that a wide-ranging genus may be associated with squirrels on only a limited part of its range, and only a few of its species may be involved in this manner, e.g. *Nosopsyllus* on the Indian subcontinent. As a result, it is necessary to consider the distribution of *all* the species in those genera in which some members parasitize squirrels, and to consider the precise regions in which this phenomenon occurs. This information is also summarized in the table. Further, since some of the Nearctic genera richest in species are restricted to the mountains of Mexico and Middle America (and the northern tip of South America), this Temperate Middle American Subregion has been treated separately from the rest of the Nearctic Region.

The Australian Region is omitted from Table 9 not only because squirrels do not occur there, but because genera of fleas associated with these hosts elsewhere are likewise absent. *Medwayella* is the nearest known representative and it is found no

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[4] In the original description this species was referred to as *O. howardi bolivari*.

TABLE 9

Distribution of fleas of arboreal and semi-arboreal squirrels, i.e. excluding fleas of chipmunks, spermophiles, etc., with total numbers of genera and species per constituent families. (Fleas of volant hosts deleted)

		Nearctic					
	Family totals	Temp. Mid. Amer.	(Other)	Palae-arctic	Oriental	Ethio-pian	Intro-duced†
Hystrichopsyllidae							
Total number genera in area	45	10^{6H-2*}	25^{10H-2*}	18^{10H}	4^{H-2*}	3^{H}	
Total number species in area for those genera (all hosts)	443	34^{*}	110^{*}	191^{H}	63	69	
Number of local genera infesting squirrels anywhere	4	1^{H}	4^{H}	1^{H}			
Total number species in such squirrel-genera (all hosts, all areas)	68	49	71	49			
Number of squirrel-species in all areas	6	2	6	2			
Number of species on squirrels in specific areas	6		5	1			
Pygiopsyllidae							
Total number genera in area	33			1^{*}	10	2	
Total number species in area for those genera (all hosts)	177			2^{*}	35^{*}	14	
Number of local genera infesting squirrels anywhere	2			1^{*}	2^{*}	1^{*}	
Total number species in such squirrel-genera (all hosts, all areas)	26			5	26	5	
Number of squirrel-species in all areas	22			1	22	1	
Number of species on squirrels in specific areas	22				22		
Ceratophyllidae							
Total number genera in area	31	11^{3H-10*}	16^{8H-10*}	19^{8H-3*}	5^{3*}	2^{*}	2
Total number species in area for those genera (all hosts)	312	77^{14*}	82^{6H-14*}	105^{6H-*}	47^{*}	16	3
Number of local genera infesting squirrels anywhere	16	5^{H}	5^{2H}	9^{2H-2*}	5^{3*}	2^{*}	2
Total number species in such squirrel-genera (all hosts, all areas)	196	86^{7*}	66^{H-7*}	111^{2H-*}	88	61	66
Number of squirrel-species in all areas	81	22^{2*}	22^{H-2*}	47^{H}	40	21	12
Number of species on squirrels in specific areas	81	8^{2*}	13^{2*}	18^{H}	38	15	

H = Holarctic genus or species.
* = One genus or species occurs in more than one area.
† = Genera like *Monopsyllus* and *Nosopsyllus*, which include some introduced species.

closer than Indonesia and the Philippines. The Neotropical Region is also not included, for no squirrel-fleas have been found there even though a few squirrels are endemic, as extensions of the Nearctic fauna in the northern mountains.[5]

From Table 9 it can be seen that only 6 of 443 species of hystrichopsyllid fleas are associated with arboreal or semi-arboreal squirrels and only 22 of 177 pygiopsyllid fleas infest such hosts. In contrast, 81 of 316 species of ceratophyllid fleas of non-volant hosts are found on these sciurids. Of the 6 hystrichopsyllid species, 5 are Nearctic and the sixth Palaearctic (Japan), while all of the 22 pygiopsyllids on squirrels are Oriental (and, as we have seen, 21 of these are in *Medwayella*).

Ceratophyllid squirrel-fleas are found in all four Regions listed, and insofar as concerns numbers of species, are better represented in the Oriental Region than in the others, and nearly as well in the Ethiopian Region as in the Nearctic and Palaearctic. However, there are significant differences in other respects, due to the fact that very few ceratophyllid genera are present in the Oriental and Ethiopian Regions, and those that do occur, infest squirrels there and elsewhere. In contrast, in the Palaearctic and Nearctic Regions, squirrel-ceratophyllid genera are not only in the minority, but generally include many species which parasitize other hosts. These points are shown by the following figures. Five of the 11 genera of ceratophyllids occurring within the Temperate Middle American Subregion infest squirrels somewhere in their range. (Four of these, namely *Kohlsia*, *Pleochaetis*, *Opisodasys* and *Orchopeas*, parasitize such hosts within the Subregion; the fifth, *Monopsyllus*, is known from chipmunks in Mexico, but species infesting tree-squirrels occur in other Nearctic subregions and in the Palaearctic.) These 5 genera include a total of 86 species, of which 22 are associated with squirrels, with 8 such species occurring within the Subregion. There are 69 ceratophyllid species in the area (90% of the total) which do not infest the sciurids under discussion. In the remainder of the Nearctic Region, there are also 5 ceratophyllid genera which include squirrel-fleas (of a total of 16), namely 4 of the 5 more southern ones, but with *Tarsopsylla* replacing *Kohlsia*, which does not occur north of the Temperate Middle American Subregion. (Moreover, the 1 or 2 squirrel-species of *Pleochaetis* are unknown north of southern Mexico.) A total of 66 species are found in these 5 genera, and 22 of these are squirrel-fleas, of which 13 occur in the Subregions in question, the residue being Temperate Middle American or Palaearctic. A total of 69 (84%) of the ceratophyllids in the Region infest other kinds of hosts. A similar picture is presented by the Palaearctic fauna. Thus, 9 of 19 genera are associated with arboreal or semi-arboreal squirrels, and these genera include 105 species, of which 47 infest squirrels somewhere within the range of the genera. However, it is important to note that these figures include *Macrostylophora*, of which only 2 of the 28 species are Palaearctic, the remainder being Oriental. There are 18 species of squirrel-fleas in the

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[5] Squirrel-fleas very likely occur in the mountainous part of South America, but have not yet been reported, although little collecting has been done there. *Pleochaetis dolens quitanus* (Jordan, 1931) has been described from *Oryzomys* Baird, 1857, and *Thomasomys* Coues, 1884, in Ecuador, while the nominate form, from Central America, is common on squirrels. It is believed that sciurids occur in that part of Ecuador. Moreover, some *Thomasomys* are arboreal, and the *P. dolens quitanus* may hence be strays from squirrels. Sciurids are found in South America as far south as northern Argentina.

Palaearctic Region, but 87 ceratophyllids which do not infest squirrels likewise occur there, and these total 83% of the species known.

The situation is quite different in the more southern Regions. In the Oriental Region, all 5 of the endemic ceratophyllids have species infesting squirrels. (As will be stressed later in another article, no ground-dwelling cricetids, which are the major hosts of ceratophyllids, occur there.) Of the 49 species of Oriental ceratophyllids, 37 are squirrel-fleas. The exceptions are largely members of *Nosopsyllus* on gerbillines and murids (which are the main hosts of the genus, there being only 6 squirrel-species, all on *Funambulus* on the Indian subcontinent). Of the 10 species of *Paraceras* known to me, only 1, an undescribed species from Indo-China, infests sciurids; the remainder parasitize carnivores or murids. However, the Formosan *P. sauteri* (Rothschild, 1914), when better known, may turn out to be a squirrel-flea, since most of the records are from arboreal carnivores.

Similarly, in the Ethiopian Region (where there also is a dearth or literal absence of ground-dwelling cricetids), ceratophyllids are relatively scarce. There are only

TABLE 10

Distribution of certain mammals in Malaya, Sumatra, Java and Borneo

Species	Malaya	Sumatra	Java	Borneo
Tupaia glis	+	+	+	+
Tupaia minor	+	+		+
Tupaia tana	+	+		+
Ptilocercus lowi	+	+		+
Callosciurus hippurus	+	+		+
Callosciurus nigrovittatus	+	+	+	+
Callosciurus notatus	+	+	+	+
Callosciurus prevosti	+	+		+
Dremomys (species)	+			+
Lariscus insignis	+	+	+	+
Rhinosciurus laticaudatus	+	+		+
Sundasciurus lowi or *S. tenuis*	+	+		+
Pithecheir melanurus	+	+	+	
Rattus (*Lenothrix*) *canus*	+	+		+
Rattus (*Lenothrix*) *rajah* or *R. surifer*	+	+	+	+
Rattus (*Lenothrix*) *whiteheadi*	+	+		+
Rattus (*Leopoldamys*) *sabanus*	+	+	+	+
Rattus (*Maxomys*) *fulvescens*	+	+	+	+
Rattus (*Stenomys*) *muelleri*	+	+		+
Echinosorex gymnurus	+	+		+
Hylomys suillus	+	+	+	+

2 such genera with a total of 16 species. Of these, 15 occur in the endemic African genus *Libyastus*, with 14 species on tree-squirrels. The remaining endemic ceratophyllid is a murine-species of *Nosopsyllus* (which genus is well represented in the Palaearctic Region of Africa on murines and gerbillines).

Certain wide-ranging and introduced forms, such as *Nosopsyllus fasciatus* (Bosc., 1801), *N. londiniensis* (Rothschild, 1903), *Monopsyllus anisus* (Rothschild, 1907), etc., have been treated in a special column in Table 9. The first-named is of probable Indian origin; the remainder Palaearctic.

TABLE 11

Species of fleas of non-volant hosts* known from Malaya, Java, Sarawak and Sabah.
(Wide-ranging fleas of commensals excluded)

Malaya	Java	Sarawak	Sabah
Medwayella robinsoni	*Medwayella robinsoni*	*Medwayella robinsoni*	
Medwayella phangi		*Medwayella phangi*	
Medwayella calcarata		*Medwayella calcarata*	
Medwayella dryadosa	*Medwayella dryadosa*		
		Medwayella veruta	*Medwayella veruta*
Medwayella limi	*Medwayella javanica*	*Medwayella batibacula*	*Medwayella* n. sp. '*A*'
Medwayella n. sp. '*F*'		*Medwayella loncha*	*Medwayella* n. sp. '*D*'
		Medwayella rhaeba	*Medwayella* n. sp. '*G*'
			Medwayella n. sp. '*H*'
			Gryphopsylla hopkinsi
*Lentistivalius insolli**			*Lentistivalius vomerus*
			Pygiopsylla tiptoni
Stivalius jacobsoni	*Stivalius jacobsoni*		*Stivalius* n. sp. '*A*'
Stivalius klossi	*Stivalius klossi*		
		Stivalius mjoebergi	*Stivalius mjoebergi*
	Stivalius (s. s.) *cognatus*		
Macrostylophora hastata	*Macrostylophora* n. sp. '*J*'		*Macrostylophora borneensis*
			Macrostylophora n. sp. '*A*'
Macrostylophora levis	*Macrostylophora* n. sp. '*K*'		*Macrostylophora* n. sp. '*B*'
			Macrostylophora n. sp. '*I*'
Paraceras n. sp. '*A*'	*Paraceras javanicum*		*Paraceras pendleburyi*
Syngenopsyllus calceatus	*Syngenopsyllus calceatus*		
Syngenopsyllus n. sp. '*A*'			
Neopsylla dispar	*Neopsylla sondaica*		*Neopsylla luma*
	Neopsylla n. sp. '*A*'		
Palaeopsylla apsidata	*Palaeopsylla laxata*		
Rothschildiana smiti	*Rothschildiana kopsteini*		
	Cratynius bartelsi		*Cratynius audyi*
			Cratynius crypticus
Totals: 10 Genera 17 Species	11 Genera 15 Species	2 Genera 8 Species	10 Genera 18 Species

* = *Lentistivalius insolli* is a bird-flea, but other members of the genus infest mammals.

TABLE 12

Numbers of genera of fleas shared by Malaya, Java or Borneo (Sabah and Sarawak only), with names and zoogeographic (regional) affinities of absentees. (Fleas of non-volant hosts.*) (Wide-ranging fleas of commensals excluded)

Area and numbers of genera	Malaya			Java			Borneo (Sabah and Sarawak)		
	Numbers shared	Unknown in Malaya	Affinities of absentees	Numbers shared	Unknown in Java	Affinities of absentees	Numbers shared	Unknown in Borneo	Affinities of absentees
Malaya (10)	–	—	—	9	*Lentistivalius**	Australian	7*	*Syngenopsyllus* *Palaeopsylla* *Rothschildiana*	All Palaearctic
Java (11)	9	*Stivalius* (s. str.) *Cratynius*	Australian Palaearctic	–	–		7	*Stivalius* (s. str.) *Syngenopsyllus* *Palaeopsylla* *Rothschildiana*	Australian 3 = Palaearctic
Borneo (10)	7	*Gryphopsylla* *Pygiopsylla* *Cratynius*	2 = Australian Palaearctic	7	*Gryphopsylla* *Lentistivalius* *Pygiopsylla*	All Australian	–	–	–

* = The species of *Lentistivalius* in Malaya is a bird-flea, unlike other members of the genus.

C. Notes on the Fauna of Sumatra and Java as Compared with Malaya and Borneo

In the text above, it was noted on a significant number of occasions that certain mammals known from Malaya, Sumatra and Borneo had not been recorded from Java. This discrepancy is quite striking, as can be seen from Table 10, which lists the relevant distribution for many of the mammals we have been discussing (but is not to be considered a complete tally for all mammals). Of the 20 species or groups of mammals cited as occurring in both Malaya and Borneo, no less than 19 (95%) are likewise found in Sumatra, but only 8 (40%) of these are known from Java as well. All those listed for Java are known for at least Sumatra and Malaya. Insofar as concerns any of the hosts under discussion in this article and for which reasonable data exist, I know of no instance of a Javanese mammal which is present in Malaya or Borneo but which is unrepresented in Sumatra. (This is not to imply that there are no endemic Javanese rodents or other mammals, for there are, e.g. *Rattus* (*Maxomys*) *bartelsi*. Similarly, the leopard is absent from Sumatra and Borneo but inhabits Java, while wild oxen are unknown on Sumatra but occur in the other three areas. These mammals are not being discussed here.) There is one rat that is listed by Ellerman (1941) for Java and Borneo but not Sumatra, and that is *R.* (*Maxomys*) *cremoriventer*.[6] However, Ellerman had no Malayan record for this species either, and we now know it is abundant there. It therefore seems likely that it is present on Sumatra as well.

It is regretted that so little is known about Indonesian fleas that it is impossible to prepare comparable data on Siphonaptera for analysis.

The fleas of Malaya, Java and Borneo are analyzed further in Tables 11 and 12, but Sumatra is deleted therefrom because of the insufficiency of data. In Table 11 are listed the relevant fleas we have been discussing, showing the species known from Malaya, Java, Sarawak and Sabah. The data deal with non-volant hosts, but *Lentistivalius insolli* Traub, 1950, a bird-flea, is included because other members of the genus infest mammals. It is pointed out that *Stivalius jacobsoni* and its sibling new species are regarded as belonging to an unnamed genus, and *S. mjoebergi* and *S. klossi* are tentatively placed in another such genus.

Three of the species of *Medwayella* occur in both Malaya and Sarawak, but these are unknown in Sabah. Of the 5 *Medwayella* in Sabah, only 1 has been found in Sarawak. However, 5 *Medwayella* listed for Sarawak are unknown farther north. There are 18 species, representing 10 genera, known from Sabah, but only 2 of these are reported from Sarawak, where only a total of 8 species, including 7 *Medwayella*, have been recorded.

There are 10 relevant genera and 24 species of fleas occurring in Borneo (Sarawak and Sabah). Seven of these genera are also found in Malaya, the exceptions being the Bornean *Gryphopsylla*, *Pygiopsylla* and *Cratynius*, and the Malayan *Syngenopsyllus*, *Rothschildiana* and *Palaeopsylla*. The Malayan genera not reported from Borneo do occur in Java, however. Twenty-one of the Bornean species are unknown in Malaya, but at least 5 close relatives are found there instead.

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[6] Oddly enough, this species is apparently not mentioned by Misonne (1960) and is not listed in his index. Since he cites Java as the southern limit of what he calls (*Maxomys*), and *R. cremoriventer* is common on Borneo, it is difficult to know where he would place this taxon.

Nine of the 10 Malayan genera occur in Java. Five Javanese species, representing 4 genera, are also found in Malaya. Seven of the 10 Javanese genera are found in Borneo. Three of the 14 genera represented in Table 11 are found in all 4 areas. However, if Sabah and Sarawak are considered as an entity, this figure is raised to 6.

Table 12 deals with the numbers of genera shared by Malaya, Java and Borneo, treating two of the areas at a time. The corresponding absentees are listed, and their apparent zoogeographic affinities indicated. For example, 9 of the 11 Javanese fleas are also found in Malaya, and the 2 that are unreported there are *Cratynius*, which is of Palaearctic ancestry (as noted in the Discussion below), and *Stivalius* (*s. str.*), whose origins are presumed to be in the Australian Region. The high correspondence of genera between Java and Borneo (7 of the 10 Bornean and 11 Javanese) and between Malaya and Borneo (7 of 10) is noteworthy. Three of the genera present in Malaya and Java but unknown in Borneo are of Palaearctic affinity.

III. DISCUSSION

A. Introduction

With the foregoing data and observations as a background, attempts are now made to answer, in sequence, the following major questions:

(1) Is the intimate association between fleas of the genus *Medwayella* and squirrels of the tribe Callosciurini a fundamental one, or are *Medwayella*-fleas really tupaiid-parasites secondarily infesting squirrels?

(2) Is *Medwayella* derived from stock with a Palaearctic origin or affinities?

(3) What are the geographic origins of callosciurine squirrels of the Malayan and Burmo-Chinese Subregions, and of their fleas?

(4) What are the geographic origins of the fleas infesting the subgenus *Rattus* and insectivores in those Subregions, and of those hosts?

(5) What are the zoogeographic inter-relationships of Malaya, Sumatra, Java, Sarawak and Sabah, and the Philippines, as indicated by the fleas and their hosts?

B. Callosciurines as the True Hosts of *Medwayella*

Callosciurines and tupaiids are not only the most common hosts of *Medwayella*-fleas, more so than those of any other groups of mammals, but their ranges roughly parallel that of this genus of Siphonaptera. Both callosciurines and tupaiids are found in all the countries and major islands of the Oriental Region, and both are absent from Luzon. These squirrels have a somewhat greater range, however, reaching Ceylon, Formosa, Celebes (Wallacea) and even to the fringes of the Palaearctic in the mountains of southern Asia, where there are no tupaiids. *Medwayella* has been found in all the areas where these two groups of mammals are both present, with the exception of India, where there has been little or no collecting of fleas in the relevant habitats. Further, except for Formosa, adequate data on fleas are lacking from those areas where callosciurines occur in the absence of tree-shrews. It may therefore be that *Medwayella* occurs there as well.

Analysis of the data, however, indicates that callosciurines, and not tree-shrews, are the true or characteristic hosts of *Medwayella*. Thus, in Malaya, where we have collected extensively, one species (*M. calcarata*) was never taken on *Tupaia*, and *M. limi* was rarely found on that host, and only 10% of the *M. dryadosa* came from *Tupaia*. It is true that 50% of the *M. phangi* there were from tree-shrews, but 49% came from callosciurines. Even if one considers only the fleas collected on *Tupaia* in Malaya, 80% of the records deal with but one species of *Medwayella*, but there are 6 species of *Medwayella* in the area (Traub, 1972a). In the few instances where *Tupaia* served as the major host for certain fleas, e.g. *Lentistivalius vomerus* and *Stivalius mjoebergi* on Mt Kinabalu in Sabah, there were no *Medwayella* found.

Another reason to minimize the possibility of a basic or original connection between tupaiids and *Medwayella* is that there is no correlation between the numbers of species of fleas and those of the host, nor are there any geographical or ecological features to account for such a discrepancy if there were such a relationship. For example, there are only 2 species of *Tupaia* in Malaya, and the only other tupaiid is *Ptilocercus*. None of these are known to harbour specific fleas, and it is unreasonable to expect that 6 species of local *Medwayella* could have evolved on tupaiid hosts (even extinct ones) and today exhibit so little evidence of such a relationship. It is true that there is a wealth of tupaiids on Borneo and that 3 species of *Medwayella* are currently known from these hosts, but there is little evidence of specificity in their relationships. Moreover, although 9 species of *Medwayella* are known from Bornean callosciurines, there are a number of such squirrels which have not yet been examined for Siphonaptera, and these may also be hosts of *Medwayella*. In contrast, sundry *Tupaia* there have been relatively frequently checked for fleas. As for the other tupaiids, neither *Dendrogale* nor *Urogale* has characteristic fleas, but nothing seems to be known about the ectoparasites of *Anathana* Lyon, 1913.

Like the tree-shrews, the numbers of species of *Medwayella* are at their maximum in Borneo, and decrease markedly according to the distance from the heart of the Malayan Subregion. This is true for callosciurines only with respect to the Philippines and Celebes, for these squirrels are well represented to the north of the known range of *Medwayella*. However, this apparent correlation between tupaiids and *Medwayella* is believed to be coincidental and an independent reflection of the geographic limits and centre of development of each group. Further discussion of this point, concerning *Medwayella*, will be presented below.

C. Origin and Affinities of *Medwayella*

Inasmuch as *Medwayella* is a pygiopsyllid, the distribution of the family is highly relevant. Two-thirds of the genera and 60% of the species of pygiopsyllid fleas of non-volant hosts are found in New Guinea or Australia, or both, and of these, one genus (*Pygiopsylla*) occurs in Borneo as well (i.e. *P. tiptoni*). Nearly 89% of the known species are found in the Australian, Wallacean or Oriental Regions, and 80% of the total number of species are found in the archipelagoes and islands of those Regions. It is my conviction that these figures imply more than the mere fact that the pygiopsyllids have reached the heights of development in that part of the world, but rather that they arose in the New Guinea–Australian Subregion and from there extended west and north through the 'Malfilindo' Archipelagoes towards and into Asia (Traub, 1966; in press; in prep.). The occurrence of one endemic genus each in the Ethiopian and Neotropical Regions is regarded as evidence of ancient faunal links, via island-hopping mammal-hosts, between the Southern Continents, and hence serving in support of the theory of Continental Drift (Traub, in press; in prep.). The low number of pygiopsyllids on the Asian mainland, the dearth of Palaearctic species (only 1, a Japanese member of the wide-ranging *Lentistivalius*, which is believed to be a relatively generalized and ancient taxon) and the absence of Nearctic forms all reinforce this hypothesis of origin of pygiopsyllids in the Australian Region and militate against derivation from 'holarctic' fleas, with subsequent penetration south and east from the Asian mainland.

The affinities of the Bornean species, *P. tiptoni*, are also pertinent in this regard. The closest members of the genus, in both the geographic and taxonomic sense, are on New Guinea, and belong to a group associated with native murines, not the commensal species of the subgenus *Rattus*. The host of *P. tiptoni*, *Rattus baluensis*, may belong to the subgenus *Bullimus* according to Misonne (1969), who considers it most closely related to *R.* (*B.*) *xanthurus* of Celebes. Other data on fleas and mammals suggestive of faunal connections between New Guinea, Celebes and Borneo are discussed elsewhere (Traub, in prep.).

It is therefore hypothesized that the forebears of *Medwayella* originated in the Australian Region, but I believe that the genus itself arose in the Malayan Subregion (probably Borneo, where it is best represented) and became associated with callosciurines and travelled towards and onto the mainland as their squirrel hosts moved back and forth on their peregrinations, having penetrated the islands from the opposite direction (see below, p. 423). As has been noted above, the acme of evolution of *Medwayella* has been in Borneo (at least 11 species), and the number of species dwindles markedly toward the periphery of its range (1 species on Palawan, another on Mindanao, 2 in Indo-China). Of the other 4 genera or species-groups of pygiopsyllids represented on Borneo, 1 is endemic (*Gryphopsylla*), 2 include but 2 species (with only 1 reaching the continent), and 1 (*Lentistivalius*) is a wide-ranging taxon with 1 non-Asian species on the mainland. Insofar as concerns fleas of non-volant hosts and excluding *Medwayella*, only 6 species of pygiopsyllids are found on the continent, and 3 of these infest commensal rats.

The low number of pygiopsyllids in Asia militates against the possibility that the family (or even just *Medwayella* alone) arose on the continent. If the pygiopsyllids were indeed of Asian ancestry, one would have to postulate that their forebears were practically exterminated, probably along with their hosts, or else because of competition with other fleas. There is no evidence for such an origin. For example, no fossil marsupials have yet been found in Asia, and it is believed that pygiopsyllids were probably aboriginally associated with marsupials (Holland, 1969; Traub, 1968; Traub, in prep.). Further, the contemporary Asian pygiopsyllids certainly lack characters associated with primitive fleas such as possession of multiple combs of spines (Traub, 1968; 1972b) and as mentioned below, *Stivalius s. str.*, the taxon associated with *Rattus* (*R.*) *rattus* and which includes 3 species in Ceylon and India, is rather specialized, suggesting geological youth. The relative dearth of Asian pygiopsyllids becomes more significant when it is realized that the most varied terrain on earth is found in the continental territory of the Oriental Region, i.e. habitats ranging from true desert, plains, swamps and equatorial rain-forest to mountain-deserts, coniferous forests, alpine meadows and subarctic scree and arctic wastes. Why did the aboriginal hosts of such theoretical pygiopsyllids, and/or the secondary hosts adopted by such pygiopsyllids as the original ones became extinct, fail to exploit such opportunity for radiation and evolution? The failure cannot be easily ascribed to 'competition', for there are vast areas of India, Thailand and Indo-China which have not been pre-empted by cricetids, or which are unsuitable for sciurids, and these should have been available for the hosts of Asian pygiopsyllids. (Incidentally, it is pointed out that no cricetid-pygiopsyllid is known.) In New Guinea there is an enormously diversified pygiopsyllid fauna infesting murids, and hence it would be expected that ancestral Asian pygiopsyllids, if there were any, would be associated there with murids, particularly since it is often claimed (as Darlington, 1957, stated) that murids '. . . have replaced most cricetids in tropical Asia and in Africa'. If this is so, it is strange that the murid fauna of the Indian Subregion and the South East Asian Mainland is so sparse. Thus, this huge and diversified area includes only 15 genera of murids, but there are 12 such genera in the Philippines alone, of which no less than 10 are endemic, while only 8 of the Asian ones are endemic. In New Guinea there are 22 murine genera, with 16 found nowhere else (Traub, in prep.). Moreover, the Asian murids which allegedly replaced the cricetids, and which undoubtedly are highly successful where they do occur, have failed to adapt themselves to the deserts or the upper reaches of the mountains of Asia. This is in contrast to what the murids have accomplished on the heights of the mountains of Africa and in the deserts of Australia. It is evidence of this type that makes me wonder (Traub, in press; in prep.) if, like the pygiopsyllids, the murids did not really have their origin, or early development, in the Australian Region, as mentioned below (p. 430).

There is another observation that seems to support the contention about the origin of *Medwayella*, and that is the fact that this genus is apparently essentially restricted to the foothills and lower parts of the mountains within its range, rather than on the upper reaches and mountain peaks. Thus, of the 21 *Medwayella* known to me, none are truly characteristic of the really temperate climes above 6000 ft elevation in the mountains of the Malayan Subregion. There have been no *Medwayella* taken at 4500 ft, or higher, on Mt Kinabalu, for example, even though squirrels are common in the area. In contrast, species of *Macrostylophora*, a ceratophyllid, are commonly found on callosciurines at such elevations, and as indicated below, that genus is of Palaearctic extraction. It seems fitting that a genus of New Guinean-Australian affinity should be restricted to relatively mild climes, rather than a temperate or near-alpine one, which is characteristic of ceratophyllids. Along these lines, it is of interest that, unlike the condition in the 'holarctic' regions, there is apparently no true alpine fauna of mammals, and virtually none for fleas, on the high mountains of New Guinea or on Mt Kinabalu. What happens is that as one ascends the upper levels of these mountains, the only pertinent and faunal change noted is that fewer species of mammals are present, but no new kinds appear to replace them. This is also true of the fleas on Mt Kinabalu, and to a great extent, on the New Guinea mountains as well. The fact that there are a few distinctive alpine fleas in New Guinea, and that these are pygiopsyllids, supports my belief that the family has a more ancient history in the New Guinean and Australian Subregions than in the Oriental Region.

There are other indications that *Medwayella* is a relatively youthful taxon with roots in the Australian Region that became adapted to callosciurines in the Insular Malayan Area. *Medwayella* not only lacks primitive characters such as abdominal ctenidia, but is actually specialized in certain respects, e.g. the lumacaudate process, the structure of the aedeagus (Traub, 1972a) and the modifications of the pronotal comb in the manner of the fleas of tree-squirrels (Traub, 1972b). The generalized pygiopsyllids, in contrast, are all in the Australian Region, and not within the range of *Medwayella*.

D. Geographic Origins of Callosciurine Squirrels and Their Fleas

1. The Callosciurine Fleas

While the zoogeographic evidence indicates that *Medwayella* is descended from fleas of Australian–New Guinean origin, the data clearly indicate otherwise for the other callosciurine fleas and for the squirrels themselves. Considering the data on Siphonaptera first, it will be recalled that there are 3 other genera of fleas, *Macrostylophora*, *Syngenopsyllus* and *Paraceras*, all ceratophyllids, associated with these squirrels. (A fourth such genus, *Nosopsyllus*, occurring in India, is found on *Funambulus*, which is not in the Callosciurini.)

It is emphasized that the family Ceratophyllidae is definitely a northern one, for out of 31 genera[7] with species infesting non-volant hosts, 28 (90%) occur in the Nearctic or Palaearctic Regions, while 8 of these are truly Holarctic (Traub, in prep.). There are 316 relevant species in this family,[8] and of these, 252 (80%) occur in the Nearctic or Palaearctic Regions (including 6 which are literally Holarctic). There are no Neotropical ceratophyllid fleas of non-volant hosts, and no ceratophyllids at all in the Australian Region. Only 5 genera (16% of the total) occur in the Oriental Region, but only 2 (*Syngenopsyllus* and *Hollandipsylla*, with 3 and 1 species respectively) are endemic. The others (*Nosopsyllus*, *Paraceras* and *Macrostylophora*) have Palaearctic representatives and the first is mainly Palaearctic. There are but 2 Ethiopian genera: *Libyastus* (15 species) and *Nosopsyllus* (with only 1 of 46 species occurring there). It is noteworthy that even bird-ceratophyllids are absent from the Australian Region, despite the fact that some are notoriously far-ranging, e.g. *Dasypsyllus stejnegeri* (Jordan, 1929), described from the Arctic, is known from Mexico and the Falkland Islands, and *Dasypsyllus gallinulae* (Dale,

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[7] This total includes *Ceratophyllus* Curtis, 1832, in which 45 of 46 species infest birds, but 1 Holarctic species, usually placed in this genus, parasitizes carnivores.

[8] The 2 *Nosopsyllus* and 1 *Monopsyllus* of commensal rats are included in these totals.

1878) is not only Holarctic, but has been found in Borneo, the Philippines and Malaya.

In the Southern Hemisphere, the majority of ceratophyllids are squirrel-fleas, but this is not so in the Northern one. In the Nearctic Region 6 out of 17 genera of ceratophyllids (35 %) have some species of fleas that infest tree-squirrels (including flying-squirrels) or scansorial sciurids; in the Palaearctic, 8 of 18 genera (40 %). The number of such species of squirrel-fleas in those Regions totals 81 of 196 (41 %). In the Southern Hemisphere, by contrast, at least 14 of 15 *Libyastus*; all of the *Macrostylophora* (28 species, of which 26 are Oriental and 2 Palaearctic) and *Syngenopsyllus* (3 species); the monotypic Bornean *Hollandipsylla* and 6 of the 12 Oriental species of *Nosopsyllus*[9] infest squirrels. Only 1 of the 10 *Paraceras* is known to be a squirrel-flea (in Indo-China), but 3 of the species are Palaearctic. In all, 53 of the 64 (83 %) Oriental and Ethiopian ceratophyllids are squirrel-fleas, 38 species in the former Region and 15 in the latter.

In so far as concerns the Oriental ceratophyllids of sciurids, virtually all in the Malayan and Burmo-Chinese Subregions are associated with the tribe Callosciurini. *Hollandipsylla neali* Traub, 1953, is the only exception, and it is known only from a flying-squirrel. In the Indian Subregion, the known squirrel-fleas are nearly all *Nosopsyllus*, on *Funambulus* (Funambulini) with but 1 *Macrostylophora* reported (from Ceylon, also on *Funambulus*). In the Palaearctic (Himalayan) region of West Pakistan, *M. fimbriata* and 2 monotypic new genera of ceratophyllids are associated with flying-squirrels. (No Callosciurinae are known to occur in the area.)

Except for *Medwayella*, the only squirrel-fleas associated with callosciurines anywhere, or occurring in the Malayan or Burmo-Chinese Subregions at all, are ceratophyllids. The points outlined above indicate that the Ceratophyllidae is a family that originated in the Northern Hemisphere, implying that the Oriental members were derived from Palaearctic roots. Further consideration of the genus *Macrostylophora*, and the data on squirrel-fleas in general, both strongly suggest that such an inference may be correctly drawn. *Macrostylophora* is the dominant genus associated with Callosciurinae, outnumbering the species of *Medwayella*, and having much broader geographical and ecological ranges than does that pygiopsyllid. Since 26 of the 28 species of *Macrostylophora* are found in the Malayan or Burmo-Chinese Subregions, and the bulk of these are endemic to an island, or a relatively restricted geographic area, like Malaya, it is logical to assume that many of these species actually arose there. Nevertheless, the morphological and taxonomic features of *Macrostylophora* clearly indicate Palaearctic origin. Thus, the two new genera of Himalayan (hence Palaearctic) ceratophyllids share some of the cardinal features of *Macrostylophora*, though otherwise abundantly distinct, and a redefinition of the last-named taxon is necessary as a result. Further, these (and other) new Palaearctic taxa also indicate the need for revision of the classification of such ceratophyllid genera as *Callopsylla* Wagner, 1934, and *Citellophilus* Wagner,

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[9] The remaining Indian *Nosopsyllus* (6 species) infest murines and gerbillines, as do the Palaearctic species (33 species). The sole Ethiopian species is a murine-flea.

1934 (both Palaearctic), and the Holarctic *Monopsyllus*, none of which occur in the Oriental Region.

The data on squirrel-fleas summarized in Tables 8 and 9 (pp. 411 and 413), outlined above (pp. 414 and 422), also reinforce this contention of Palaearctic affinity. The third family of fleas associated with squirrels (but not Callosciurinae) is that of the Hystrichopsyllidae, and while squirrel-fleas are rare in the group, involving only 6 of 443 species, it is significant that this family too is common in the North. Thus, 74% of the known genera are found in the Nearctic or Palaearctic Regions. The 4 genera of hystrichopsyllids (3 Nearctic and 1 Holarctic) associated with squirrels also have species which infest peromyscines (Cricetidae), and this is also true of 5 of the ceratophyllid-genera (4 Nearctic and 1 Holarctic), which parasitize tree-squirrels. Moreover, in 7 out of these 9 genera, the species infesting tree-squirrels are in the minority (e.g. 1 of 23 *Kohlsia* and 2 of 52 *Rhadinopsylla*). This suggests that these genera are not only of northern origin, but that they originally were associated with cricetids, rather than sciurids. The hystrichopsyllids in question are nest-fleas, and this likewise indicates that the connection with squirrels is not primary. Inasmuch as 22% of the species of ceratophyllids infest tree-squirrels and the other sciurids under consideration, it would seem that there has been a long connection with such hosts even if their forebears had parasitized other mammals. The fact that at least 14 of the 16 Ethiopian ceratophyllids (15 *Libyastus* and 1 *Nosopsyllus*) are parasites of tree-squirrels also bespeaks of a basic and long-term association. The Palaearctic affinities of the Ethiopian species is clear from their morphology. Jordan (1936) when describing *Libyastus*, placed it near the Holarctic *Tarsopsylla*, and the single *Nosopsyllus* closely resembles the many Palaearctic members of the component subgenus.

The very great distance between the Ethiopian squirrel-fleas and the epicentre of *Macrostylophora*, coupled with the fact that ceratophyllid fleas occur on the equally remote squirrels in the Temperate Middle American Subregion, also argues for Palaearctic (or Holarctic) rather than Oriental origin of *Macrostylophora*. The dearth of other Oriental ceratophyllids points in the same direction. Squirrel-fleas account for 37 (76%) of the 49 species of Oriental ceratophyllids, and 31 (84%) of 37 in the Malayan and Burmo-Chinese Subregions. The preponderance of squirrel-fleas in the ceratophyllid fauna in the Oriental Region, together with the low number of taxa on various hosts, as compared to the Palaearctic, suggests an original entry from the North, and a relatively recent one at that.

2. Origins of Callosciurines

If the ancestral *Macrostylophora* are of Palaearctic origin, what of the aboriginal callosciurines? The Oriental Region and Celebes house so many kinds of sciurids compared to the rest of the world that it is easy to wonder whether the family could have arisen there. Thus, the Callosciurini (which barely extends beyond the Oriental Region into the periphery of the Palaearctic) includes approximately 13 genera and

48 species.[10] The great bulk of these are restricted to the S. E. Asian Mainland, the Insular Malayan Area and the Wallacean Subregion. Within their range are also found a few diurnal squirrels belonging to other tribes, as follows: (1) the monotypic and little-known *Rheithrosciurus* in Borneo, the only member of the tribe Sciurini in the entire Region, and with its geographically nearest relative in in the central Palaearctic; (2) the genus *Funambulus* (5 species), the only Oriental representative of the tribe Funambulini, which is otherwise African; (3) *Ratufa* (4 species), the only constituent of the tribe Ratufini.

The Oriental and Wallacean Sciurinae therefore total 16 genera and about 58 species, included in 4 tribes. The Petauristinae are also highly developed in the Oriental Region, with about 10 genera occurring therein (but many of these are also Palaearctic). In contrast, there is only a total of 5 genera of Sciurinae (excluding Marmotini) in Europe, Palaearctic Asia and the New World (in the classification of Simpson, 1945), but these apparently comprise 42 species. The Marmotini would add 4 genera (6 genera fide Moore, 1959), if one wanted to include marmots, spermophiles and chipmunks. None of the other Regions include more than 3 tribes of Sciurinae, with a maximum of 6 genera per tribe occurring in the Nearctic Marmotini. There is only 1 genus (2 species) of flying-squirrel in the New World. The contrast in wealth of fauna, at the generic and tribal levels, is quite striking, especially in view of the far greater land-surface and type of habitats represented in the Eurasian Palaearctic and Nearctic areas as compared to the Malayan and Burmo-Chinese Subregions and Wallacean Subregion, where the bulk of the callosciurines occur.

The fossil record is of little assistance in trying to determine whether the diversification of sciurids in the Oriental Region is due to rapid adaptation by the descendants of immigrants to a superb environment for arboreal forms or to an ancient history of autochthons. Very few fossils of any mammals are known from the Malayan and Burmo-Chinese Subregions, and there are no such sciurids. Fossils are known from the Oligocene to Recent in Europe and North America; from the Pleistocene to Recent in Asia; and from the Pleistocene in South America and the Pliocene in Africa (Simpson, 1945; Anderson & Jones, 1967; Cooke, 1968; Patterson & Pascual, 1968). Walker et al. (1968) state that ground-squirrels are known to date from the late Miocene, 'whereas the tree squirrel extends back in time possiby to the Oligocene'.

If there is a specific account of the origins and migrations of the sciurids in general, it has escaped my notice. Since the family is absent from the Australian Region, it has not been mentioned by Simpson, Tate, etc., when discussing the origins of the Australian fauna, as mentioned regarding murids below (p. 430). It is regretted that Moore & Tate, in their fine opus on Sciurinae of the Indian and Indochinese

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[10] Moore (1959) in his revisionary work on the higher classification of the Sciurinae mentions 12 genera and 6 subgenera of Callosciurini. One of his subgenera, however, namely *Tamiops*, is here treated as a genus, following Moore & Tate (1965) and Harrison (1966). In the absence of any single authoritative source, the figures for the numbers of species is based upon an analysis of a variety of references, including Ellerman (1940), Ellerman & Morrison-Scott (1951), Harrison (1968), Laurie & Hill (1954), Medway (1963), Moore (1958 & 1959), Morris (1965) and Walker et al. (1968).

Subregions (1965) did not deal with zoogeography beyond the presentation of interesting and original ideas concerning elements of the local fauna. However, elsewhere Moore did discuss aspects of the zoogeography of certain groups of squirrels, i.e. Neotropical, Nearctic and northern Palaearctic diurnal squirrels (1971b) and those of the Indian Subregion (1960). In the first article, the 'probable place of origin is shown to be the Nearctic Region for the (subtribes) Tamiina, the Spermophilina and the Marmotina'. The subtribe Sciurina, in Moore's opinion, could have arisen in either the Palaearctic or Nearctic, but the Palaearctic is stated to be the 'centre of dispersal'. In the 1960 paper, Moore reiterated (p. 5) that *Funambulus* 'has African affinities', a point first made by him in 1959. Moore (1960) also regards the Indian habitats of *Ratufa* as an extension of its range from what is here called the Burmo-Chinese Subregion.

Matthew (1915), in an enormously influential opus, expressed the view that the 'Holarctic' area was the epicentre of origin of the dispersal of vertebrates, and pointed out that while great radiation and expansion has occurred in the southern continents, the aboriginal types were invaders from the north. He summarized his theories along similar lines in 1930. Darlington (1957, pp. 488–489) considered Sumatra, Java and Borneo as 'zoogeographically . . . very recent continental islands . . . that were all connected together and to the mainland in the Pleistocene'. He clearly regarded the fauna as 'a nearly complete continental one' and including a 'rich Oriental mammal fauna', which shows the 'beginnings of the effects of isolation and limitation of area', and with extinctions resulting in a relict pattern. Darlington (1957, p. 503) believed that the Philippine mammals (except the murids) arrived via 'rather recent immigration from Borneo'. Raven (1935) also indicated that the Philippine fauna was derived from that of 'Malaysia', and Taylor (1934) had expressed similar ideas. The sciurids of the Ethiopian Region are considered by Cooke (1968) as having been of Palaearctic origin, derived from Europe, presumably in the late Oligocene.

It should be noted that while Darlington (1957) concurred with the idea that the fauna of the Australian Region and Malfilindo Archipelagoes were derived from Asia, he did not state that they necessarily arose in the Palaearctic. In fact, in 1959 he clarified and expanded this point, claiming that the 'main Old World Tropics (tropical Asia and Africa)' was the place of origin for many dominant groups of animals, including the mammals, and that from there they dispersed in all available directions. Thus in the case of murids, Darlington believed they penetrated into Australia via the Pacific Islands. Squirrels are regarded by him as another dominant group that arose in the 'Old World tropics' and dispersed from that centre, although Darlington refers only to this group in passing, and does not give particulars as to where he believes the various taxa arose. This is an interesting and impressive hypothesis, and the wealth of callosciurine fauna on the South-East Asian Mainland at first glance appears to render it solid support. However, as Darlington himself points out, it is difficult to define what constitutes the Old World tropics, and the geographic areas encompass a tremendous diversity of habitats, including deserts, a variety of forests, alpine terrain, mangrove swamps, etc. Moreover, the upper reaches on the mountains in Asia are often Palaearctic, rather than Oriental. Did the squirrels arise in the temperate or the tropical parts thereof?

In view of the dearth of information on fossil sciurids, and the complete absence of records of fleas of critical squirrels like the sole member of Sciurini in the middle of Borneo, and of Celebes squirrels, it is futile to try and decide definitively here whether sciurids actually arose on the mainland of the Oriental Region, or whether they radiated there rapidly after the arrival of aboriginal forms from the north. However, the data on Siphonaptera, outlined above, do suggest certain relevant conclusions, particularly: (1) the number and diversity of ceratophyllid fleas parasitizing squirrels indicates that the basic association is an old one, and that it reached its height at the generic level in the Palaearctic and Nearctic Regions; (2) the bulk of the fleas of Oriental squirrels are definitely of Palaearctic origin; and (3) the squirrels of the Insular Malayan Area and Wallacea were derived from forms that entered from the Asian Mainland; and (4) their entry there was comparatively recent, geologically speaking.

Thus, the Ceratophyllidae, the main family of fleas which is associated with squirrels throughout their range, clearly had its roots in the Northern Hemisphere, as we have seen. More than 50% of the genera in the family include species infesting relevant squirrels, and 41% of the species in those genera actually parasitize such hosts. However, 61% of those genera are found in the Palaearctic or Nearctic Regions, even though a small proportion of the genera of squirrels dwell there, e.g. more than two-thirds of the Sciurini are found in the Oriental and Wallacean Regions. Moreover, some of these genera are quite specialized, at times monotypic, and restricted to squirrels. Only 31% of the ceratophyllid genera with squirrel-fleas inhabit the Oriental Region, despite the wealth of hosts. Since there are so few ceratophyllids at all in the Insular Malayan Area, and these are comparatively of little diversified at the generic level, it would appear that the entry thereto by squirrels was in relatively recent geological times, and that only a few pioneers were involved. (Of course the period must have been long enough to permit the local development of a large number of species within these few genera, as the squirrels radiated within the Region.) It is pointed out that if these migrant-hosts from the north were not sciurids, then they left no trace behind in the Oriental Region in so far as concerns fleas, for *Macrostylophora*, *Syngenopsyllus* (and *Hollandipsylla*, the petauristine flea from Borneo), which are kin, have no near allies in the Region (although they do in the Palaearctic, on squirrels). The fourth genus of ceratophyllid in the Malayan Subregion, *Paraceras*, which is occasionally (1 species) associated with sciurines, is not closely related to these other ceratophyllids. It is reiterated that not all the Oriental squirrel-fleas are of northern affinity, and I believe that on these islands, probably Borneo, the squirrels, working their way south and east from the mainland, encountered *Medwayella* or its prototype, which had migrated (with other pygiopsyllids) in the opposite direction, from Celebes or the Australian Region, and that *Medwayella* then accompanied the callosciurines as they moved back and forth between the mainland and the islands, and towards Palawan and Mindanao.

Zoogeographic data on the sciurid-fleas of Formosa may also provide a possible clue about the origin of the squirrels. Both diurnal squirrels (callosciurines) and flying-squirrels (*Petaurista*) occur on that island, and the former harbour *Macrostylophora* but the latter are infested with *Monopsyllus argus* (Rothschild, 1908), a Palaearctic flea which is found as far east as Japan, where it is also found primarily on *Petaurista*. The most common *Macrostylophora* is *M. liae*, also known from Fukien on the Chinese mainland. In both areas this flea is associated with *Tamiops swinhoe* and *Callosciurus erythraeus* (Pallas, 1779). The Formosan callosciurines and their fleas are of Oriental affinity, but what is the significance of the Palaearctic species of flea on *Petaurista*? These giant flying-squirrels range from Kashmir and Szechuan to Borneo and the Far East, and are usually found in the mountains of the Oriental Region but also occur in the foothills, as low as 1500 ft elevation, as in Malaya. In Pakistani Kashmir (in the Palaearctic Region) a new genus of ceratophyllid of Palaearctic affinity is found on *Petaurista*, while a second such new genus parasitizes *Hylopetes* in the same area. No characteristic fleas have been found associated with any flying-squirrels in Malaya, and within the last few years these hosts have been intensively studied, and examined for fleas, by the U.S. Army Medical Research Unit (Malaya). It may be significant that these USAMRU collections were primarily from the lower elevations. The only petauristine-flea known from the Oriental Region is *Hollandipsylla*, a ceretophyllid of Palaearctic ancestry collected in the truly cool climes of Mt Kinabalu. The available data therefore suggest that the flying-squirrels entered the Oriental Region from the north, bringing their stocks of Palaearctic fleas with them, and that in the tropical areas they lost their fleas and have not yet become affiliated with Siphonaptera of native origin. In the Himalayas, however, where the Palaearctic merges with the Oriental Region, *Hylopetes* has acquired *Macrostylophora fimbriata*, which of course is a member of an Oriental genus (associated with callosciurines) and is of northern ancestry, and has transported it to Pakistani Kashmir, where callosciurines are unknown.

The apparent absence of callosciurines in that part of the Himalayas, where at least 3 genera of petauristines occur, is a fascinating problem. Perhaps the callosciurines became extinct there, but it seems more likely they were never present, due to one or more of the following possible factors: (1) the callosciurines are too youthful a group to have yet penetrated; (2) the available habitats are themselves of such recent derivation that only the more mobile petauristines could successfully exploit them following extinction of the original fauna; and (3) the petauristines entered from the Palaearctic climes of the northern and eastern branches of the Himalayas and hence were adjusted to the rigorous climes, unlike the callosciurines, which as a group are associated with far milder climates.

If (3) were the answer, it would not explain why callosciurines were absent from the forest in the lower elevations of these particular areas in Kashmir. (The occurrence of *Funambulus* in the plains just a few miles away is attributable to the African origins of funambulines. The faunal connections between the arid areas of West Pakistan, and the deserts of Iran, leading to North Africa, are reasons for placing this part of the Indian Subcontinent in the Southeast Palaearctic Subregion.) If the second factor above was the reason, then the 'ecological islands' in the mountains of Gilgit, Dir, etc., scattered throughout the deserts of Central Asia must have become isolated a relatively short time ago.

Various of the points made above indicate that the sciurids in the Insular Malayan Area were relatively recent immigrants. As mentioned elsewhere (Traub, in prep.), I believe that in certain parts of their range they entered into competition with sundry giant tree-rats which had entered earlier, moving from a New Guinean focus, and that, as a result, the tree-rats became extinct in certain areas. It is striking that the giant tree-rats have reached the apex of their development in areas where squirrels are unknown (New Guinea, Flores, Luzon). Moreover, there are only a few regions where the two both occur, e.g. Mindanao and Celebes, but I have no data if they actually co-exist in the same micro-habitats.

E. Geographic Origins of *Rattus*-Fleas and Their Hosts

1. *Rattus*-Fleas

There are five families of fleas associated with rats of the genus *Rattus* in the Oriental Region, namely the Pygiopsyllidae, Leptopsyllidae, Pulicidae, Hystrichopsyllidae and Ceratophyllidae, and the first three of these occur in the Australian Region as well (and probably in the Wallacean). If the margins of the Palaearctic Region, such as the southern U.S.S.R., are added (and where pygiopsyllids are absent), this territory encompasses the geographic limits of the wild (non-commensal) members of the genus *Rattus*.[11]

As we have seen, the Pygiopsyllidae is overwhelmingly a family of the Southern Hemisphere, with the preponderance of genera and species (especially endemic ones) in the Australian Region, but with fair representation in the Insular Malayan Area. At least 16 of the 28 genera infesting mammals in the Australian Region are prime parasites of rats. Notably, 15 of these are restricted to New Guinea, where they parasitize a variety of murid genera but only relatively few of these are found on the genus *Rattus* (Traub, in prep.), and those that do so are invariably associated with subgenera other than (*Rattus*). It is worth emphasizing that Laurie & Hill (1954) and Lidicker & Ziegler (1968) do not list any native members of the subgenus *Rattus* on New Guinea only commensal forms are known. The sixteenth genus of rat-pygiopsyllids of New Guinea, *Metastivalius* Holland, 1969, is also found in Australia, and includes a few species infesting the subgenus *Rattus*, but most of the members occur on other kinds of rats.

Similarly, all but one of the murid-pygiopsyllids listed in Tables 4 and 7 (pp. 402 and facing page 406) are parasites of true forest-rats rather than of the subgenus *Rattus*. Moreover, the records from the subgenus *Rattus* pertain to wild forms of (*Rattus*) occurring in secondary forest, and not from commensal rodents or species of rats typical of the grasslands, indicating these fleas had strayed from their proper hosts. The exception is *Stivalius* (s. str.), such as *S. cognatus*, and these characteristically infest the subgenus *Rattus* and usually are associated with subspecies of *R.* (*R.*) *rattus*.

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[11] Misonne (1969), unlike earlier workers, does not consider the genus *per se* to be represented in Africa, and has raised the older 'subgenera' to full generic level.

The degree of specialization exhibited by the sundry pygiopsyllid rat-fleas is also of relevance. Many of the New Guinean murid-fleas are highly modified with respect to the shape of the head, and the development of helmets or crowns of spines or spiniform bristles which are apparently tailored to fit the nature of the hairs of the host (Traub, 1968; 1972b). Such adaptations suggest a long evolutionary history on these particular hosts, and seem to imply the groups are relatively ancient. The bulk of the pygiopsyllids of the forest-rats of the Indo-Malayan area (*Gryphopsylla* and *Stivalius s. lat.*), on the other hand, are much more generalized, and seem to have a younger history. (It is pointed out, however, that they lack the primitive features seen in some of the Australian and New Guinean pygiopsyllids, especially those associated with marsupials.) The fleas of *Stivalius* (*s. str.*) are quite distinctive in the family in that the sclerotized inner tube of the male is elongate, while the genitalia of the female are correspondingly modified (Traub, 1972a). A specialization of this type does not imply antiquity but merely a development that occurred subsequent to the association with *R. rattus*, since it does not occur in related taxa.

There are, then, four points about the pygiopsyllids of rats in the Insular Malayan Area that are in accord with the concept of the origin of the Pygiopsyllidae in the Australian Region and subsequent movement with their hosts through the Malfilindo Archipelagoes towards Asia. These are: (1) the relatively small number of such rat-fleas in the area, i.e. far less than in the Australian Region; (2) the progressive decrease in the number of pygiopsyllids on rats towards the periphery of the Oriental Mainland of Southeast Asia, and the absence of these fleas in the adjacent Palaearctic; (3) the close association of the bulk of the rat-pygiopsyllids of the Insular Malayan Area and the adjacent mainland with forest-rats rather than the subgenus *Rattus*, paralleling the case in New Guinea; (4) the significantly lower degree of specialization in the fleas of these forest-rats as compared with those of New Guinea.

As a corollary to this hypothesis, it might be suggested that *Stivalius* (*s. str.*) had a similar focus of origin and path of migration, and that the same is true of their characteristic hosts, *R.* (*R.*) *rattus*. Before dealing with this possibility, it is necessary to review the data on other fleas of the subgenus *Rattus* and of the rats themselves. The Leptopsyllidae on rats are instructive in this regard. The family is primarily a northern one, and of the 19 genera known, 16 (84%) occur in the Palaearctic or Nearctic Regions, with 4 of these truly Holarctic, 15 genera in the Palaearctic and but 5 in the Nearctic (Traub, in prep.). There are no Neotropical forms and only 2 genera occur in the Ethiopian Region, with 1 of these Palaearctic and the other endemic for Madagascar. There are 5 Oriental genera but only 1 is endemic (*Cratynius*). As noted in Section II.B.4 above, the leptopsyllids associated with rats are mainly in the subfamily Leptopsyllinae, especially in *Leptopsylla*, *Sigmactenus* and *Peromyscopsylla*. The other genera of leptopsyllids infest primarily cricetids, with a few exceptional species in the subfamily Amphipsyllinae attaching to rats in the Southeastern Palaearctic Subregion. Seventeen of the 18 species of *Peromyscopsylla* infest Palaearctic or Nearctic cricetids, but the single exception is a Palaearctic rat- or *Apodemus*-parasite which (or an undescribed sibling thereof) has been recently found in the mountains of Luzon on rats of the subgenus *Rattus*, accompanied by another Palaearctic leptopsyllid, a *Frontopsylla*

Wagner & Ioff, 1926 (Amphipsyllinae). Ten of the 15 species of *Leptopsylla* are known from murines, and about 3 of these are known from rats in the Ethiopian and Palaearctic Regions. A derivative of *Leptopsylla* (*Pectinoctenus*), namely *Sigmactenus*, is of especial interest because the 3 species extant are found on the genus *Rattus* in Borneo, New Guinea and the Philippines, respectively, with at least the last one infesting the subgenus *Rattus*. It appears definite, then, that faunal extensions of this predominantly northern family, which largely parasitizes non-murids, exist in the Malfilindo Archipelagoes and New Guinea, and that they are associated with *Rattus* or (*Rattus*). (A leptopsyllid of insectivores on Borneo and Java will be mentioned below.)

Another family which is well developed in the Northern Hemisphere but which has exceptional representation in the Insular Malayan Area is the Hystrichopsyllidae. Only 4 genera (9% of the total) are found in the Oriental Region and 3 of these are better known in the Palaearctic, namely *Palaeopsylla* (Ctenophthalminae), *Neopsylla* (Neopsyllinae) and *Stenischia* Jordan, 1932 (Rhadinopsyllinae). The fourth, *Rothschildiana* (a neopsylline) has been reported only in Malaya and Java, on *Rattus*. Eighty-two per cent of the genera of Neopsyllinae are restricted to the northern regions, and these taxa include 65% of the species. Of the *Neopsylla* for which we have information, 9 species (31%) are Oriental, with 3 (10%) in the Malayan Subregion (1 each in Malaya, Java and Borneo). Eight (89%) of the Oriental species infest *Rattus* (of several subgenera, including the subgenus *Rattus*), and the 7 Palaearctic members of the *N. stevensi*-group apparently parasitize the subgenus *Rattus*. While both *Rothschildiana* are *Rattus*-fleas, the bulk of the few available records are from the subgenera *Lenothrix* and *Maxomys*.

Palaeopsylla is mentioned below (Section F.1), since the genus is characteristic of insectivores. The precise hosts of *Stenischia* are in doubt since there have been relatively few reports, and while some species have been collected on insectivores (in Japan, Formosa, Nepal), I have some specimens from rats, not only in Formosa but for a new species from Thailand (1 specimen!), the only Oriental record for the genus.

From the foregoing it is clear that the Oriental hystrichopsyllids have Palaearctic roots and that most of the species involved are associated with *Rattus*, and often the subgenus *Rattus*. However, the zoogeography of the Hystrichopsyllidae in the Malfilindo Archipelagoes and the Australian Region cannot be explained by that concept alone, for 2 endemic genera, each representing distinct tribes, are found in Australia, infesting marsupials. There are no known hystrichopsyllids on New Guinea nor anywhere in the Malfilindo Archipelagoes save Java and Borneo. Such a discontinuous distribution is difficult to explain on the basis of hosts, for cricetids and insectivores, and not rats, are the major hosts of hystrichopsyllids in the Northern Hemisphere, and cricetids are apparently absent in the Malayan Subregion and the rest of the Austral-Asian Archipelagoes, while insectivores are poorly represented in that Subregion and Wallacea, and absent (except for commensal shrews) in the Australian Region. Moreover, endemic subfamilies or tribes of Hystrichopsyllidae are also found in South America and in Africa, separated by thousands of miles from their nearest relatives and 'expected' hosts. A distribution of this type, in my view, is evidence of aboriginal faunal 'island-hopping' connections between the Southern Continents and renders further support for the theory of Continental Drift (Traub, in press; in prep.). Those who do not accept the hypothesis tend to explain the phenomenon in terms of original continuous distribution, followed by extinctions to create the gaps, and evolutionary changes to account for the phylogenetic modifications.

The Ceratophyllidae, a northern family as noted above, is primarily represented in the Insular Malayan Area by squirrel-fleas, but there also are data suggesting both a connection with rats and a Palaearctic origin therefor. The genus *Paraceras* includes Palaearctic and even European forms, but 7 of the 10 species occur in the Oriental Region, and 2 of these (both undescribed) presumably infest rats (Thailand, Malaya). The Malayan species is known only from about 6000 ft elevation, where it is common on *Rattus* (*Stenomys*) *bowersi* and *R.* (*Leopoldamys*) *edwardsi* (Thomas, 1882). A Bornean species infests the ferret-badger, *Melogale* (*Helictis*) *orientalis everetti* (Thomas, 1895). Another species associated with carnivores such as viverrids and (*Helictis*) Gray, 1831, is found in the Oriental parts of Formosa.

The Pulicidae, more than any other group of fleas, has a discontinuous distribution among the Southern Continents, and is rather poorly represented in the north. Thus, among the Xenopsyllinae, 78% of the 88 species are found in the Ethiopian, Oriental or Australian Regions; 78% of the 23 species of Pulicinae are known from the Neotropical, Australian or Ethiopian Regions; 73% of the 11 Archaeopsyllinae are from the Ethiopian or Oriental Regions (Traub, in prep.). The broad but discontinuous range even exists at the generic level: *Echidnophaga* Olliff, 1886, includes 6 endemic Australian species (on marsupials), 5 in the Ethiopian Region and 5 in the Palaearctic (Southwestern and Eastern Subregions). *Xenopsylla* is the most widely dispersed genus in the family, but, notably, there are no representatives in the New World. There are no less than 43 endemic Ethiopian species on gerbillines and murids, and 20 mammal-*Xenopsylla* are indigenous to the Palaearctic. In Australia there are 2 species (*X. vexabilis* and an allied form) associated with rats of the subgenus *Rattus*, and *X. vexabilis* is also known from New Guinea, Java, the Philippines (all on the subgenus *Rattus*) and from the Oriental Mainland of Southeast Asia, where it infests *R.* (*Bullimus*) *berdmorei*. (*X. cheopis* (Rothschild, 1903) and other species of fleas of commensal rats have been transported to many parts of the world and are ignored herein. *X. vexabilis* belongs in the synanthropic category, at least in part, and has been introduced into Hawaii, for example, but it may also be indigenous in parts of its known range and hence is treated as being relevant.) On the basis of the range of *X. vexabilis*, it would be easy to conclude that this species represents an original entry from the Palaearctic or Indian Subregion into the Oriental Mainland of Southeast Asia and hence into and throughout the Austral-Asian Archipelagoes, primarily via the subgenus *Rattus*.

Supporting this theory is the fact that a related species, *X. nesiotes* (Jordan & Rothschild, 1908) occurs on rats of the subgenus *Rattus* on Christmas Island, south of Java. However, the occurrence of a highly modified and endemic species of *Xenopsylla* on an autochthonous rat in New Guinea and another such from the mountains of New Guinea complicates the zoogeographic picture. Such indigenous specialized forms suggest antiquity, and since other pulicids (*Echidnophaga*) are known in Australia, and share a common distribution at the generic level with Africa, it may be that these *Xenopsylla* have their roots in the Australian Region. It should also be noted that the affinities and hosts of the Palaearctic *Xenopsylla* (and even the Indian ones) indicate the possibility that the movements of the aboriginal *Xenopsylla* (and their hosts) were from Africa towards India, and not the reverse (a direction counter to the belief of virtually all mammalogists). Moreover, there are no endemic *Xenopsylla* known in Malaya, Burma, Tibet and China, so that no northern or western links for the Thai and Indo-Chinese *X. vexabilis* are apparent. Regardless of where *X. vexabilis* or its forebears originated, it seems to have accompanied commensal rats over much of their peregrinations. Thus, in New Guinea it has only been found in a few coastal areas, always on the subgenus *Rattus*. The Philippines records are also from commensal rats, in Central Luzon.

Regardless of such problems, however, on the whole the data on Siphonaptera strongly suggest that, with the exception of the pygiopsyllids (and perhaps the pulicids as well) the fleas infesting rats of the genus *Rattus* of the Australo-Asian Archipelagoes and the Oriental Mainland of Southeast Asia were derived from Palaearctic stocks. The evidence is strongest in the case of fleas infesting certain groups of *Rattus* and the subgenus *Rattus*. The low numbers of fleas involved at the generic and species level for all of the families in the Insular Malayan Area, suggest relatively recent entry. The relative wealth of mainland and Palaearctic taxa in the case of the hystrichopsyllids, leptopsyllids and ceratophyllids supports this view of youth, and the same is true for the pygiopsyllids when considering New Guinea as the possible ancestral homeland.

2. Geographic Origins of the Australo-Asian Murids and *Rattus*

The question of the origin of rats is being treated at length in the article dealing with fleas and Continental Drift (Traub, in prep.), and this subject will at present essentially be limited to relevant highlights. Practically all of the leading naturalists and mammalogists believe that the rats arose on the Asian mainland and then penetrated the various members of the Australo-Asian Archipelagoes, including Australia and New Guinea, progressing by rafts or 'island-hopping'. Simpson as early as 1940 could confidently state that it 'is generally conceded that . . . (the) . . . Australian rodents are of Asiatic origin and reached Australia without a continuous land-bridge' (p. 763). In 1961 Simpson elaborated on this point, and based upon the data of Tate (1936, 1951) and others, postulated that the rodents of the Australian Region could be divided into 4 groups, with different histories. One such group, the 'Old Papuans', include genera whose forebears are supposed to have reached New Guinea by multiple invasions from the East Indies in the period from the Miocene to the Pliocene. Another group, the 'Old Australians', are thought to have been derived from perhaps a single immigrant in the Miocene. A third group comprises the hydromyine rats, which Simpson believes evolved in New Guinea from an Asiatic ancestor in the Miocene, with later descendants moving to Australia and the Philippines. The fourth group is the one with which we are presently concerned, and this includes 'local members of the very widespread genus

Rattus'. A batch of autochthonous *Rattus* are believed to be derived from one or two migrants 'through the East Indies' in about the early Pleistocene. Much later, commensal rats entered in several waves, through the activities of man.

Asian ancestry of the murids (and all other indigenous mammals) of various parts of the Australo-Asian Archipelagoes was also proposed or accepted by Taylor (1934) for the Philippines; by Raven (1935); Darlington (1957; 1959) and Keast (1968; 1969). Misonne (1969) in a major and highly significant opus on 'African and Indo-Australian Muridae' also concurred regarding the Asian origin of these rats, particularly concerning 'Southeast Asia', but he seems to include Borneo and the neighbouring islands in 'Southeast Asia'. Nevertheless, he clearly agrees that the route of travel was towards the Australian Region, etc. However, there has not been complete unanimity on this score, for Ellerman (1940 and 1941) suggested that the rats arose in the Australian Region and migrated towards the Asian mainland, and that they 'are among the most archaic of mammals'. These ideas of Ellerman's were very strongly criticized by Simpson in 1945, and since Ellerman offered no rebuttal when (1949) referring to Simpson's opus, perhaps he had come to accept Simpson's views.

It is also the concensus that African mammals were derived from Asian or European stocks (Darlington, 1957; Cooke, 1968; Keast, 1969). Misonne (1969) also believes that the African murids are descended from Asian taxa.

The data on Siphonaptera, and a review of the zoogeography of mammals, have led me to seriously question whether the murids arose in Asia, or even the adjacent islands or underwent their major evolution there. In fact, I believe that their origin, or at least their aboriginal development as such, may have been in the Australian Region (Traub, in press; Traub, in prep.) and that this is where they acquired their pygiopsyllids and that they then moved, together with their fleas, via Celebes towards the Philippines, and in another line, towards Borneo and the mainland. According to this hypothesis, evolution of new forms continued through the eons as the murids moved back and forth between the islands, but progressing towards the continents, resulting in giant tree-rats and other endemic forms of ancient lineage in Celebes, Flores and the Philippines, etc., and the subsequent development of the genus *Rattus*. Various subgenera of *Rattus* appeared on some of the islands, probably including Borneo, and also on the mainland, and these migrated eastward to New Guinea, as well as westward and northward. This theory would account for the relative sparsity of murid genera on the Asian mainland, alluded to above (p. 422). As a corollary to this hypothesis, it is suggested that the African murids were also derived, to a great extent, from island-hopping stock from the Australian Region before the continents drifted too far apart. This would explain how the pygiopsyllids entered Africa, for there is no trace of the family in the Palaearctic Region between India and central Africa. Similarly, it is my belief that there were limited faunal exchanges of marsupials, complete with stephanocircid helmet-fleas and pygiopsyllids, and some hystrichopsyllids, between Australia and South America. Evidence from the Siphonaptera and their hosts also has led me to believe that the murids (and indeed most groups of rodents and insectivores) are a more ancient group than is generally believed, and that the rats were in New Guinea at far earlier times than postulated by Simpson. These are all highly controversial points, and the data and arguments are being presented and developed elsewhere (Traub, in press; Traub, in prep.). They are mentioned here to emphasize that the Siphonapteran data nevertheless do strongly support Simpson's views (1961) about the relative ages of the various rats in his 'groups' of Australian and New Guinean murids and, particularly, that the *Rattus* group was the youngest, and that it entered the Australian Region from the western islands. Thus, the hystrichopsyllid and leptopsyllid fleas infesting rats in the Insular Malayan Area are obvious extensions of the Palaearctic Region, as we have seen, and as has been noted for the squirrel-fleas, etc. Further, they seem to be relatively recent evolutionary phenomena, e.g. *Rothschildiana* is a development of *Neopsylla*; and there has been little differentiation at the generic level in general, and little speciation. There is also a close association with the subgenus *Rattus*, as in the case of *Sigmactenus*, which has ranged as far east as New Guinea. Moreover, regardless of where the pulicid *Xenopsylla vexabilis* and the pygiopsyllid *Stivalius s. str.* actually arose, there can be no doubt that they are intimately connected with the subgenus *Rattus*, and probably *R.* (*R.*) *rattus* at that. They have been found together with (*Rattus*) in widely separated areas, and the species of *Stivalius s. str.*, at least, have differentiated at the subspecies level in a classical geographical manner. (Names for subspecies of *X. vexabilis* exist but their validity is in some doubt.) The degree of phylogenetic changes suggests geological youth for these taxa of fleas, indicating that their hosts are either young themselves or new in the areas. The fact that the species of *Stivalius s. str.* have specialized genitalia of a type not seen in related forms, and are restricted to *R.* (*R.*) *rattus*, makes me believe the taxon and its host developed together, even though the *Stivalius* are the descendants of fleas that originated in the Australian Region.

F. The Origins of Insectivore-Fleas and Insectivores of the Insular Malayan Area

1. Shrews and Shrew-Fleas

In many parts of the world, shrews (Soricidae) are abundant in numbers of individuals and species (and the scientific names proposed for them). This is true of the Northern Hemisphere in general, but not in parts of the far north. (Shrews even occur, to a limited extent, in the desert.) Several genera are endemic to the Ethiopian Region and the same is true for Ceylon. Soricids are poorly represented in the islands of the Malayan Subregion, but extend as far as Celebes. Native or wild forms are absent in Australia, New Guinea, and adjacent islands, all of South America save for the Nearctic extension therein; although the commensal *Suncus* Ehrenberg, 1833, has been introduced into some Pacific islands. *Crocidura* is probably the sole genus occurring in native form in the Wallacean Subregion, but its range extends northward to the Philippines and westward to and over much of the Palaearctic (but apparently not very far north in Asia) and thence deep into Africa. It is difficult to estimate the number of species in the various areas, for the genus is in sore need of revision. As Ellerman & Morrison-Scott (1951) point out, 110 names at the purported species level have been proposed for Africa alone.

Medway (1963) lists 2 species of *Crocidura* and 2 non-commensal *Suncus* for Borneo, and 1 of each of these also occurs in Malaya (Harrison, 1966). A third genus of soricid, *Chimarrogale* Anderson, 1877, a water-shrew, is found on Borneo, and Malaya and Sumatra, and may be represented thereon by various subspecies of a single species that is Palaearctic, extending as far as Japan, Szechuan and Kashmir.

Unfortunately, the only available data on fleas of soricids of the Malayan Subregion concerns *Crocidura*, and little information is available there, i.e. the occurrence of an endemic species of *Palaeopsylla* on that host in the mountains of Malaya, and another on Java. Since 85% of the 27 *Palaeopsylla* are Palaearctic, and the other 3 Oriental members of the genus are in South China, the Palaearctic origins of these fleas seem as clear as those of their hosts.

2. Erinaceids and Their Fleas

There are 2 members of the Erinaceidae that are found in parts of the Insular Malayan Area, namely the *Echinosorex* Blainville, 1838, the moonrat or gymnure and *Hylomys* Müller, 1839, the lesser gymnure. Both are monotypic and are present in Malaya and Borneo. The northern limit of *Echinosorex* is southern Thailand, and it is also found on Sumatra. *Hylomys* ranges throughout much of the Oriental mainland of Southeast Asia, and occurs on Sumatra and Java as well. So far as I am aware, there are no records of fleas from *Echinosorex*, nor from mainland *Hylomys*. A leptopsyllid, *Cratynius*, has been collected from *Hylomys* on Java (1 species) and Sabah, on Mt Kinabalu (2 species, both from the same locality). It is unusual for 2 species of fleas of a single genus to be found on the same species of host in one area, particularly a monotypic one with no local related taxa. As reported by Hopkins & Traub (1955), both Bornean species of *Cratynius* were very difficult to collect. Only 13 specimens are extant, even though 46 individuals of the presumed host, *Hylomys*, were examined carefully for fleas. Since 85% of the known specimens are from *Hylomys*, and since hundreds of other mammals in the same local area were checked to little or no avail, *Hylomys* nevertheless does seem to be the characteristic host, particularly since it is also associated with *Cratynius* on Java. Still, it is pointed out that recent collections of *Cratynius* on Java include specimens from the subgenus *Rattus*. Moreover, very few such commensal rats or wild forms of (*Rattus*) were examined by us on Mt Kinabalu. The absence of records of *Cratynius* from the mainland may represent inadequate collecting of *Hylomys*, for we have searched thousands of *R.* (*Rattus*) in various habitats in Malaya. There are not many species of leptopsyllids which infest insectivores, although a *Leptopsylla* from the Soviet Union is supposed to parasitize a shrew, and further study may disclose *Cratynius* is a murid-flea after all, like so many of its relatives.

Another unusual feature is that Leptopsyllidae are unknown in Malaya and are poorly represented in the Insular Malayan Area, although occurring on rats there, as previously noted. *Cratynius* is in the Leptopsyllinae, although it is placed in a distinctive tribe. While an endemic taxon, its roots are definitely Palaearctic, as indicated above, whether or not it is a true insectivore-flea.

G. Fleas and Their Hosts in the Insular Malayan Area

It has been shown above that except for the pygiopsyllids, virtually all of the fleas in the Malayan Subregion are clearly of Palaearctic origin, and the same is apparently true for, at least, the non-murid rodent-hosts. However, the data also have bearing on the apparent route of entry into the various parts of the Insular Malayan Area of both fleas and hosts, as well as upon certain features of the history of the fauna therein.

1. *Zoogeographic Inter-Relationships of Malaya, Sarawak, and Sabah*

Although Malaya and Borneo share a significant sciurid and murid fauna, the features in common are more notable for Malaya and Sarawak than Malaya and Sabah, and there appear to be some notable differences between the rodents and fleas of Sabah and those of Sarawak. Borneo may also have a somewhat closer faunal affinity with Malaya (and Sumatra) than with Java, while there is little to suggest any major entry into Borneo from Indo-China. Data bearing on these points may be summarized as follows.

Fifty per cent of the genera and 36% of the species of squirrels reported for either Malaya or Borneo occur in both areas. The comparable figures for murids are 43% and 41% respectively. The relationship is even more marked, for sibling species are also present, and some of the Malayan taxa reach their southern limits in that country. Of the species or species-groups treated in Table 2 (p. 398), 40% of the taxa of squirrels and 59% of the non-commensal murids occur in Malaya, Sarawak and Sabah. However, 3 of the rodents (9% of the total) are limited to Malaya and Sarawak, while 19% of the Bornean murids are found only in Sabah. One of the 18 species of Bornean squirrels is limited to Sarawak, and another is essentially so. All of the rodents common to Sabah and Malaya are likewise found in Sarawak. Relatively few of the mammals treated are shared by Indo-China and Borneo, and the exceptions (*Tupaia glis*, *Crocidura*, *Hylomys suillus* and *Rattus* (*Maxomys*) *fulvescens*) are wide-ranging and are found in Malaya as well.

Moreover, similar conclusions may be drawn from the records on fleas, particularly as summarized in Tables 11 and 12 (pp. 416 and 417). Thus, 3 species of *Medwayella* are common to Malaya and Sarawak but none of these are found in Sabah. (One, *M. robinsoni*, is found in Java, Sumatra and Thailand as well.) Only 12·5% of the 18 species of Sabah fleas (representing 10 genera) are known from Sarawak, while 88% of the 8 Sarawak fleas belong to *Medwayella*. The differences in the Sarawak and Sabah Siphonapteran fauna may reflect lack of adequate data from Sarawak, especially in the mountains, but the degree of diversity imply a definite zoogeographic phenomenon.

Ninety per cent of the 10 Malayan genera of fleas treated in this article are known from Java (and the sole exception is a species of *Lentistivalius* which infests birds). There are only 2 genera in Java which are not represented in Malaya, and only 4 such in Borneo. Seventy per cent of the 10 genera reported for Borneo are found in Malaya. There is also significant similarity at the species level. Malaya (with a total of 17 relevant species) and Java (with 15) share 5 species, representing 4 genera. Two of these are in *Medwayella*. Moreover, at least 3 of the other Malayan species are closely allied to the Javanese. There is a minimum of 5 Bornean species of fleas which are near relatives of Malayan fleas.

Malaya and Java share 3 genera which are absent from Borneo, and all are of Palaearctic affinity. The 3 Bornean genera which are unknown in Java are all pygiopsyllids and hence with presumed ancestry in the Australian Region. Three of the genera unreported from Malaya are such pygiopsyllids.

None of the species of fleas we have been discussing are shared between Indo-China and Borneo. What relationships there are occur, at best, at the generic level, and lead to Malaya, and to a lesser extent, to Java and Sumatra. There are only 3 species common to both Indo-China and Malaya, belonging to 3 genera (*Stivalius s. lat.*, *Neopsylla* and *Macrostylophora*).

The data on both mammals and fleas, then, suggest that there is a significant degree of difference between the fauna of Sabah and Sarawak, and that the former tends more towards endemicity than the latter. It also appears that Sarawak shares more with Malaya than Sabah. Since so many elements of the Sabah fauna are apparently of Palaearctic ancestry, but with no real links with Indo-China, it seems that these probably entered Sabah from the south or southwest, originating from Malaya or Java or Sumatra, and did not penetrate from the north, from Indo-China or Formosa. Except for wide-ranging taxa, like *Callosciurus* and *Macrostylophora*, or *Neopsylla* (which occur throughout the intermediate areas), there is little in common in the pertinent fauna of Borneo on the one hand, and Indo-China and Formosa on the other. However, there is the notable case of the new species of Bornean *Macrostylophora* ex *Dremomys* on Mt Kinabalu, which also is known from Formosa (as a distinct subspecies). Nevertheless, *Dremomys* does occur over much of the Oriental Mainland of Southeast Asia (although not reported from Java or Sumatra). At our current level of knowledge, it is impossible to determine what such a distribution means, although it is this sort of circumstance that accounts for my regarding the foothills and lowlands of Formosa as belonging to the Oriental Region.

2. The Relative Poverty of the Javanese Mammalian Fauna

A glance at Table 10 (p. 415) discloses that many of the mammalian hosts listed for Malaya, Sumatra and Borneo are unrecorded from Java. Thus, of the 19 species or groups listed for Malaya, Sumatra and Borneo, only 8 (42%) are likewise represented on Java. The comparative sparsity of the Javanese mammalian fauna is well known. For example, Taylor (1934, pp. 98–99) stated: '. . . while *Ptilocercus*, *Dendrogale* and *Tana* [now placed in *Tupaia*—R.T.] are present in Borneo and Sumatra . . ., they appear to be totally wanting in Java. It suggests that Java was separated prior to the separation between Borneo and Sumatra or Borneo and the Asian Mainland'. Dammerman (1929) discusses the distribution of various mammals in these islands, as does Darlington (1957), mainly concerning the larger species. No doubt, extinctions have played an important part in the anomalous distribution, e.g. orangs and bears were present in Java during the Pleistocene but are absent today. The fauna of sciurids and rodents nevertheless seems disproportionately impoverished, and it is difficult to explain the absence of certain widespread forms by extinctions of certain elements alone. It seems clear that Java must have had a different geological history than Sumatra or Borneo. It appears likely that subsidence of vast areas in the sea, coupled with enormous volcanic action over a large area, may have resulted in mass extinctions, and that only certain elements of the fauna of the Malayan Subregion could effect entry or re-entry thereafter. There is a good correlation in the taxa of Siphonaptera between Java and Borneo or Malaya, as noted above, but in view of the dearth of data from Sumatra, definitive interpretation is impossible.

3. Zoogeographic Inter-Relationships of Borneo and the Philippines

The data on the Philippines also provide evidence of the movement of the Oriental elements of Palaearctic ancestry via the Southeast Asian mainland through Indonesia and Borneo, as well as for the view that pygiopsyllids and certain murids had their ancestry in the Australian Region. A detailed consideration of these points, including the zoogeography of Luzon, will be presented elsewhere (Traub, in prep.) but the main features concerning these islands of the Philippines which are in the Malayan Subregion may be summarized as follows. A main route of entry from Borneo into the Philippines has been via the Palawan-Calamian groups of islands. Dickerson (1928, p. 26) regarded these islands as 'faunally . . . a northern extension of Borneo'. Taylor (1934) listed a number of Oriental and Palaearctic genera of mammals as occurring in the Palawan group, including such forms as tree-squirrels, flying-squirrels, *Tupaia*, scaly anteaters, badgers, mouse-deer, etc. He also wrote (p. 60) of 'direct migration from the mainland of Borneo, via land bridges at a time when Palawan and the Calamians were a peninsula of the island'. While I am not necessarily ascribing to the land-bridge theory rather than island-hopping as a means of travel, our data firmly support the main contentions of entry from Borneo to Palawan. For example, in the Palawan area are found a new species of *Medwayella* near *M. robinsoni*; the same new species of *Stivalius* near *S. jacobsoni* known from Borneo, and a new *Macrostylophora*, all on appropriate hosts. Another route from Borneo to the Philippines seems to have been from southeastern Sabah via the Tawitawi and Samales groups of small islands and Basilan Island. Here again Taylor speaks of a peninsula, but regardless of this point, the faunal connections are clear. Mindanao and the adjacent islands have a mammalian and Siphonapteran fauna that is distinct from that of Palawan in major respects, but a large component is of Bornean origin. For example, the flying-squirrel *Petinomys* Thomas, 1908, which is known from Ceylon, South India, Burma, South China, Malaya, Sumatra and Borneo, is also found on Basilan Island, but apparently nowhere else in the Philippines. On the other hand, *Hylopetes*, a flying-squirrel of the Eastern Palaearctic Region which also occurs in the mountains of the Malayan Subregion, including Borneo, is found in the Palawan area but not elsewhere in the Philippines. Similarly, the hyosciurine *Nannosciurus* (Callosciurini), known from 1 species in Sabah, is represented by separate species on Basilan Island, and Samar, and 2 on Mindanao, but not the Palawan area.

However, unlike Palawan, Mindanao shares faunal elements, or at least a heritage, with Celebes and New Guinea. Members of the murid subfamily Hydromyinae are known only from Australia, New Guinea and the Philippines, and, indeed, Simpson (1961) suggested that two endemic genera in the Philippines (Luzon and/or Mindanao) came from New Guinean stock (although ultimately derived from Asian forebears). Huge, specialized tree-rats occur in Celebes, Ceram, New Guinea and the Philippines, although it is difficult to say how closely these are related to one another. The subfamily Phloeomyinae, which Simpson recognized in 1945, includes some of these tree-rats in the four areas and is unknown elsewhere, unless the Oriental *Chiropodomys* Peters, 1868, is placed therein. Actually, in 1961 Simpson apparently had doubts about the validity of the subfamily, for he did not refer to the name, but Anderson & Jones (1967), Cockrum (1962) and others still use Simpson's 1945 scheme of classification. Misonne (1969) likewise did not utilize the name Phloeomyinae but concurred that the genera which Tate (1936) placed here are related. Most of the murid-fleas of Mindanao are pygiopsyllids, and 2 of the 5 known genera there have definite affinities with representatives in Celebes and New Guinea.

4. Some Unusual Features about the Distribution of Callosciurine Fleas

There are several anomalous features about the distribution of the fleas associated with certain of the callosciurines under discussion. For example, although some of the same species of squirrels, such as *Callosciurus notatus* and *C. nigrovittatus*, are found from Malaya to Sabah, they are infested with very different fleas in Sabah than in Malaya, or even Sarawak. Before discussing this further, it is necessary to consider some general points about the distribution of fleas and their hosts. Certain species of fleas are found throughout the ranges of their hosts, e.g. the ceratophyllid *Orchopeas leucopus* (Baker, 1904) on *Peromyscus maniculatus* (Wagner, 1845), from eastern Canada to deep into Mexico, the Rocky Mountain area and California; *O. howardi* (Baker, 1895) on *Sciurus caroliniensis* Gmelin, 1788, all over the eastern U.S.A. to Texas. Sometimes the range of the flea extends beyond that of one host, occurring on closely related species, such as *O. howardi* on other *Sciurus* Linnaeus, 1758, all the way to southern Mexico. There are some species of fleas which fairly indiscriminately infest members of a tribe or subfamily, such as *Malaraeus penicilliger* (Grube, 1852)[12] on various voles, from northern Europe, Asia (including the high Himalayas) and Alaska; or the Holarctic *Tarsopsylla octodecimdentata* on sundry Sciurinae. In other instances the relationship seems to be between the genus of flea and the genus of host, e.g. the doratopsylline *Corrodopsylla* Wagner, 1929, on *Sorex* Linnaeus, 1758, from Europe and Japan, and Alaska to at least central Mexico. On the other hand, there are surprising examples of marked speciation of fleas infesting presumably monotypic genera of mammals, where the hosts are geographically restricted to relatively small areas and within which there are no overt factors of contemporary isolation, e.g. 4 species of *Astivalius* Smit, 1953, on

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[12] A variety of subspecies of *M. penicilliger* have been named, and some of these apparently represent distinct species, but the point still holds.

Lorentzimys nouhuysi Jentink, 1911, in New Guinea and at least 5 species of *Phaenopsylla* Jordan, 1944, on *Calomyscus bailwardi* Thomas, 1905, in the deserts of Soviet Central Asia, Iran, Afghanistan and West Pakistan.

In the case of the *Callosciurus* cited above, *Medwayella robinsoni* is the characteristic flea in Thailand, Malaya, Sumatra, Java and Sarawak, but on Mt Kinabalu these are infested with *Macrostylophora* in the absence of *Medwayella*. Moreover, in Malaya, *Macrostylophora* is not associated with these particular squirrels. It may be that at 5500 6500 ft elevation, where these *Callosciurus* were examined for fleas on Mt Kinabalu, the climate is too temperate for *Medwayella*, for no members of the genus have been found there, although they are present on the mountain at about 2000 ft elevation. The genus is rare at height of 6000 ft in Malaya.

The unusual host-specificity noted for the *Macrostylophora* on *C. notatus* and *C. nigrovittatus* on Mt Kinabalu is also worth emphasis. Even squirrels on the same trees did not share fleas. Such specificity is unusual in *Macrostylophora*, at least on the Asian mainland, where *M. hastata* has been found on several species of *Callosciurus* and on *Tamiops* Allen, 1906. *M liae* is also found on those 2 genera of squirrels.

IV. CONCLUSIONS

1. Fleas of the family Pygiopsyllidae originated in the Australian Region and from there moved north and west through the Malfilindo Archipelagoes to the mainland of Asia.

2. While the Siphonapteran genus *Medwayella* has its roots in the Australian Region, it apparently arose in the Malayan Subregion, probably in Borneo, where it is best represented.

3. *Medwayella* is a relatively youthful and specialized taxon, whose true hosts are squirrels of the tribe Callosciurini, and not tupaiids (tree-shrews), and its characteristic habitat is in the foothills and lower elevations of the mountains of the Malayan Subregion and parts of the Burmo-Chinese Subregion.

4. With the exception of the pygiopsyllids *Medwayella* and *Lentistivalius*, the fleas of squirrels of the Oriental Region have definite Palaearctic affinities, as do those of the tree-squirrels of the Ethiopian Region.

5. The callosciurines of the Insular Malayan Area and Wallacea are, geologically speaking, relatively recent emigrants from the mainland of the Malayan Subregion, which penetrated to Borneo via Sumatra and/or Java, and thence to the Philippines and Celebes, carrying their ceratophyllid fleas with them, at least as far as Palawan and Mindanao.

6. *Medwayella*, however, moved in the opposite direction, from Borneo to the mainland and as far as Indo-China, but also emigrated to the Philippines.

7. While the available evidence cannot rule out that the Sciuridae originated in the 'Old World Tropics', the data suggest the possibility that the Oriental members (or at least the Petauristinae) had Palaearctic roots and that their forebears penetrated into and radiated within the Oriental Region.

8. Regardless of the point of origin of the ancestors of the genus *Rattus* (which

may have been in the Australian Region), the members of the genus and especially the subgenus *Rattus*, are relatively youthful, and worked their way back and forth between the mainland and the Australo-Asian Archipelagoes. In the process they transported from the west and northwest, certain fleas of Palaearctic stocks. At least one of these (*Sigmactenus*) has reached as far east as New Guinea.

9. *Stivalius s. str.*, although descended from fleas of the Australian Region, has been intimately associated with the subgenus *Rattus* (especially *R.* (*R.*) *rattus*), and like *Xenopsylla* of the *X. vexabilis*-group, has accompanied these rats on many of their peregrinations.

10. The insectivores and their fleas in the Insular Malayan Area are likewise of Palaearctic ancestry and entered the islands from the Malayan peninsula.

11. The data on Siphonaptera of squirrels, rats and insectivores therefore are in accord with certain, but not all, of the contentions of Darlington (1957), Simpson (1961) and others, who believe that the mammals of the Australo-Asian Archipelagoes were derived from the Asian mainland, and that the genus *Rattus* was a late emigrant.

12. Nevertheless, study of the Siphonaptera also provide strong evidence that, contrary to the belief of virtually all mammalogists, there were ancient faunal connections, involving mammals, between the Southern Continents (albeit tenuous and transient ones, via island-hopping) and hence provide support for the theory of Continental Drift.

13. Malaya, Sumatra, Java and Borneo share many faunal features, but there are significant differences between the mammals and fleas of Sarawak and those of Sabah, with the former resembling Malaya more than does the latter.

14. Although certain species of squirrels range from Thailand to Sabah, and are infested with *Medwayella robinsoni* as far east as Sarawak, they carry different fleas in Sabah (i.e. *Macrostylophora*) and these are highly host-specific there.

15. Palawan and Mindanao have derived much of their relevant fauna from Borneo, but Mindanao also has elements of Wallacean and New Guinean stocks.

V. SOURCES

In dealing with the nomenclature and classification of mammalian hosts, a certain amount of confusion is inevitable. The scheme of classification that has received global recognition is that of Simpson (1945), and the fact that general texts on mammals even as much as 20 years later, such as Cockrum (1962), Anderson & Jones (1967), Morris (1965) and Walker et al. (1968) all follow Simpson's system demonstrate how sound and useful it was. However, parts of the classification are out of date, as indicated above, and where it was pointed out that Simpson in 1961 did not fully adhere to his 1945 format when dealing with murids. Unfortunately, there has been no general opus with an alternate, complete plan of classification and there are differences of opinion expressed amongst specialists dealing with sundry components. Another problem is due to the enormous taxonomic difficulties posed by the murids, and even Misonne (1969) in his large work on rats did not indicate precisely to which subgenus certain rats (e.g. *R. baluensis*) belong.

Accordingly, we have had to rely upon several authorities for the names and taxonomic status of the mammals mentioned in this article. The basic system of classification is that of Simpson (1945), as used by Anderson & Jones (1967), etc. For Bornean mammals, we have followed Medway (1963) and for Malayan, Harrison (1966). As applicable, and when not in conflict with the above, we have also used Ellerman & Morrison-Scott (1951) for Palaearctic taxa and Laurie & Hill (1954) for the New Guinean and Wallacean ones. In specific instances we have used the names employed by Misonne (1969) on the basis of 'latest reviser' and obvious merit, but in those cases, these have been indicated. Other exceptions have also been noted in the text.

The basic classification of Siphonaptera at the higher levels is essentially that of Hopkins & Rothschild (1962 and 1966), but since the Pygiopsyllidae, Ceratophyllidae and some other critical taxa have not yet been treated by these authorities, I have used my own ideas, down to the species and subspecies. The data presented include genera and species new to Science, since these amount to an equivalent of a minimum of 5% of the known fauna, and a much higher figure for the zoogeographic areas in question.

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VIII. LIST OF SIPHONAPTERA CITED IN TEXT

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Astivalius Smit, 1953
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Ceratophyllus Curtis, 1832
Citellophilus Wagner, 1934
Conorhinopsylla Stewart, 1927
Corrodopsylla Wagner, 1929
Cratynius Jordan, 1933
Cratynius audyi (Traub, 1952)
Cratynius bartelsi Jordan, 1933
Cratynius crypticus Hopkins & Traub, 1955
Dasypsyllus gallinulae (Dale, 1878)
Dasypsyllus stejnegeri (Jordan, 1929)
Echidnophaga Olliff, 1886
Epitedia Jordan, 1938
Frontopsylla Wagner & Ioff, 1926
Frontopsylla (*F.*) *nakagawai* Kumada & Sakaguti, 1959
Gryphopsylla Traub, 1957
Gryphopsylla hopkinsi (Traub, 1957)
Hollandipsylla Traub, 1953
Hollandipsylla neali Traub, 1953
Kohlsia Traub, 1950
Lentistivalius Traub, 1972
Lentistivalius ferinus (Rothschild, 1908)
Lentistivalius insolli (Traub, 1950)
Lentistivalius vomerus Traub, 1972
Leptopsylla Jordan & Rothschild, 1911
Leptopsylla (*Pectinoctenus*) Wagner, 1928
Libyastus Jordan, 1936
Macrostylophora Ewing, 1929
Macrostylophora borneensis (Jordan, 1926)
Macrostylophora cuiae Liu, Wu & Yu, 1964
Macrostylophora euteles (Jordan & Rothschild, 1911)
Macrostylophora exilia Li, Wang & Hsieh, 1964
Macrostylophora fimbriata (Jordan & Rothschild, 1921)
Macrostylophora hastata (Jordan & Rothschild, 1921)
Macrostylophora heinrichi Jordan, 1939
Macrostylophora idoneus (Rothschild, 1919)
Macrostylophora levis (Jordan & Rothschild, 1922)
Macrostylophora liae Wang, 1957
Macrostylophora lupata (Jordan & Rothschild, 1921)
Macrostylophora phillipsi (Jordan, 1925)
Macrostylophora pilata (Jordan & Rothschild, 1922)
Macrostylophora probata (Jordan & Rothschild, 1922)
Macrostylophora sodalis (Rothschild, 1919)
Macrostylophora trispinosa (Liu, 1939)
Macrostylophora uncinalis Jordan, 1939
Malaraeus penicilliger (Grube, 1852)
Medwayella Traub, 1972
Medwayella angustata Traub, 1972
Medwayella arcuata Traub, 1972
Medwayella batibacula Traub, 1972
Medwayella calcarata Traub, 1972
Medwayella dryadosa Traub, 1972
Medwayella javana (Jordan, 1933)
Medwayella limi Traub, 1972
Medwayella loncha (Jordan, 1926)
Medwayella phangi Traub, 1972
Medwayella rhaeba (Jordan, 1926)
Medwayella robinsoni (Rothschild, 1905)
Medwayella thurmani Traub, 1972
Medwayella veruta Traub, 1972
Megarthroglossus Jordan & Rothschild, 1915
Metastivalius Holland, 1969
Monopsyllus Kolenati, 1857
Monopsyllus anisus (Rothschild, 1907)
Monopsyllus argus (Rothschild, 1908)
Monopsyllus tolli (Wagner, 1901)
Neopsylla Wagner, 1903
Neopsylla avida Jordan, 1931
Neopsylla dispar Jordan, 1932
Neopsylla luma Traub, 1954
Neopsylla setosa (Wagner, 1898)
Neopsylla sondaica Jordan, 1931
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PRESENTED

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